536


PATRE SVO
CAROLO DARWIN
A CAR
LEGATVM ACCE
PIT
FRANCISCVS DARWIN
Harry Soane. 1888.



οἷον πέπονδεν ὄνυξ πρὸς ὅπλὴν καὶ χεὶρ πρὸς χηλήν.

Aristotle

"Itaque convertenda plane est opera ad inquirendas et notandas rerum similitudines etanaloga" *Bacon*

"Similiter posita omnia in omnibus fere animalibus" *Newton*

42
94

ON

THE NATURE OF LIMBS.

A DISCOURSE

DELIVERED ON FRIDAY, FEBRUARY 9, AT AN EVENING MEETING OF THE

ROYAL INSTITUTION OF GREAT BRITAIN.

BY

RICHARD OWEN, F.R.S.

LONDON:

JOHN VAN VOORST, PATERNOSTER ROW.

MDCCCXLIX.

Cambridge University Library
On permanent deposit from
the Botany School

ON

THE NATURE OF LIMBS.

The chief difficulty that I have encountered in the endeavour to fulfil the request with which I have been honoured by the Managers of this Institution, is one which the able Secretary will be surprised to hear I owe to him: it has been the attempt to give a plain answer to Mr. Barlow's question, 'By what title shall I announce your Lecture?'

It was not until I had written and erased two or three which first suggested themselves that I became fully conscious how foreign to our English philosophy were those ideas or trains of thought concerned in the discovery of the anatomical truths, one of which I propose to explain on the present occasion in reference to the limbs or locomotive extremities.

A German anatomist, addressing an audience of his countrymen, would feel none of the difficulty which I experienced. His language, rich in the precise expressions of philosophic abstractions, would instantly supply him with the word for the idea he meant to convey; and that word would be 'Bedeutung.' It is the 'Bedeutung' of the limbs which is my present subject; and the literal translation of the word is 'signification.'

I had written at first, 'On the Signification of the Limbs of Man and Animals;' when it occurred to me that a practical audience might deem that there was small need of a learned lecture to prove that matter, and might be disposed to think that any old Pensioner at Greenwich or Chelsea could certify better than a Professor, that 'arms and legs' signified a good deal.

Our word 'meaning,' as applied to what I shall endeavour to prove, in regard to those useful appendages, would convey as false or feeble an idea of my meaning.

'On the *idea* of the limbs' might be understood only by those who knew that the word was used in the sense it bears in the Platonic philosophy.

'Homology' seems now to be accepted as the name of that study or doctrine the subject of which is the relations of the parts of animal bodies understood by the German word 'Bedeutung;' and in the technical language of anatomical science I should define the present lecture as being: "On the General and Serial Homologies of the Locomotive Extremities." But such a title would have been comprehended only by anatomists, and I knew that your Secretary had in view the information of a more general audience, to whom such technical phraseology would be less intelligible perhaps than the literal translation of the German term.

The 'Bedeutung,' or signification of a part in an animal body, may be explained as the essential nature of such part—as being that essentiality which it retains under every modification of size and form, and for whatever office such modifications may adapt it. I have used therefore the word 'Nature' in the sense of the German 'Bedeutung,' as signifying that essential character of a part which belongs to it in its relation to a predetermined pattern, answering to the 'idea' of the Archetypal World in the Platonic cosmogony, which archetype or primal pattern is the basis supporting all the modifications of such part for

specific powers and actions in all animals possessing it, and to which archetypal form we come, in the course of our comparison of those modifications, finally to reduce their subject.

The 'limbs' to which the limits of the present Discourse confine its application, are those of the Vertebrate Series of animals; they are the parts called the 'arms' and 'legs' in Man; the 'fore-' and 'hind-legs' of Beasts; the 'wings' and 'legs' of Bats and Birds; the 'pectoral fins' and 'ventral fins' of Fishes. I take for granted that it is generally known, as it is universally admitted by competent anatomists and naturalists, that these limbs or locomotive members, which, according to their speciality of form, have received the above special names, are answerable or 'homologous' parts: that the arm of the Man is the fore-leg of the Beast, the wing of the Bird, and the pectoral fin of the Fish. This special homology has been long discerned and accepted; but the general homology of the parts or their relation to the vertebrate Archetype, in short their 'Bedeutung' or essential nature, is not generally known. Some of the keenest wits and deepest thinkers amongst the anatomists of the German Philosophical School have endeavoured to penetrate the mystery, and have propounded the views which have resulted from such their attempts. But those views have never received the sanction of even partial assent; and, if the conclusion to which I have arrived be the correct one, such assent has not been unreasonably withheld.

It must be owned, however, that the non-acceptance of these generalizations has been due more to indifference and to the non-appreciation of the value of the inquiries, than to a rigorous investigation of their merits. Very few of the exact conclusions as to the general homology of parts of the skeleton of animals have been admitted with thorough comprehension and fruition of the discovery by the actual cultivators of Natural History in this country;

so that I can scarcely appeal to an example in illustration of my meaning with any hope that it will prove such to more than a very small portion of my hearers.

Some however may understand and assent to the proposition that "the basilar part or process of the occipital bone in human anatomy is the 'centrum' or body of a cranial vertebra." Now, by virtue of this truth, mark what the human anatomist comprehends! First, that the '*pars basilaris*' is not a process in the proper signification of the term, but a self-subsistent, independent element of the skull; whereby he is prepared for its primitive appearance as a distinct part in the embryo, and as a persistent distinct 'bone' in all the cold-blooded Vertebrata. He further recognises it to be a member of the same series of bones as the flat bodies of the cervical vertebræ, the thick bodies of the dorsal and lumbar vertebræ, and the broad bodies of the sacral vertebræ; and he understands why it differs from the other 'processes of the occipital bone' by its primitive relation to the embryonic '*chorda dorsalis*.' All this, and much more comfortable knowledge of the '*processus seu pars basilaris ossis occipitalis*,' is implied by the definition of its general homology, *i.e.* of its essential nature, signification, or 'Bedeutung'; and it is precisely the same kind of knowledge which I imply by the word 'nature' in reference to the limbs.

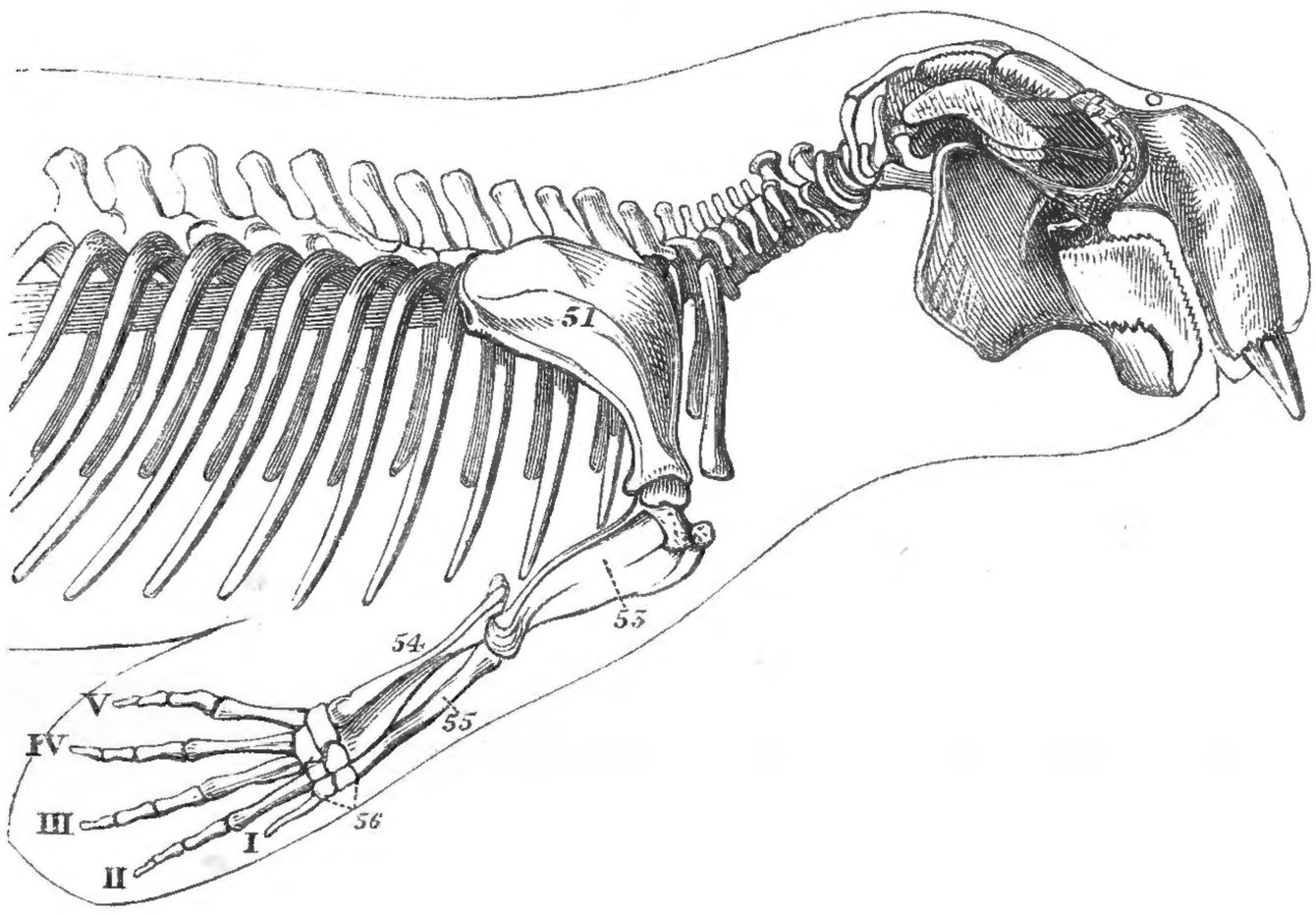
The parts to which I here refer, and to which alone the reasoning will apply that leads to the desired conclusion in the present lecture, are those in the Vertebrated animals, serving chiefly for locomotion, but sometimes adapted to other offices. Many and multiform parts answering these purposes are present in the Invertebrated animals; but their framework is formed out of a distinct system of hard parts from those employed in the Vertebrata. Here it is the internal or endo-skeleton: in the Invertebrata it is the hardened skin, the dermo- or exo-skeleton.

The hard parts of the leg of a Crab or an Insect may be 'analogous' to the bones of the limb of a Quadruped, but they are not 'homologous' with them; and where there is no special homology, there can be no relations of a higher or more general homology between the parts*.

The Vertebrated animals enjoy as extensive and diversified a sphere of active existence as the Invertebrated. They people the seas, and can move swiftly both beneath and upon the surface of water: they can course over the dry land, and traverse the substance of the earth: they can rise above that surface and soar in the lofty regions of aërial space.

The instruments for effecting these different kinds of locomotion—diving and swimming, burrowing and running, climbing and flying—are accordingly very different in their configuration and proportions. The simplest form

Fig. 1.



External form and skeleton of the pectoral fin of the Dugong (*Halicore indicus*).

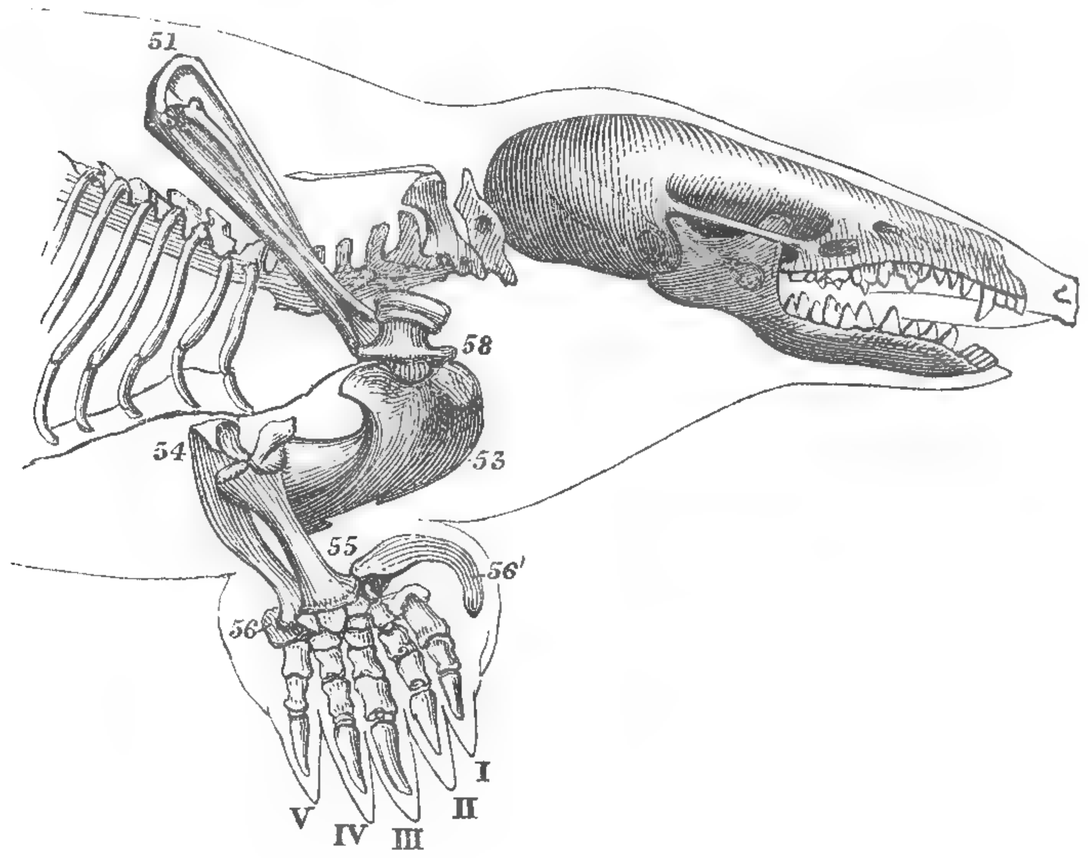
of the locomotive member is that of the fin. The marine mammal called Dugong here offers us an example of such (fig. 1). It is a strong, stiff, short, broad, flat, and ob-

* The parts termed 'femur,' 'tibia,' 'tarsus,' &c. in Entomology

tusely pointed paddle or oar; without other apparent joint than that which unites it to the body it has to propel: a joint permitting that degree of rotation with the oblique stroke that makes the movement of the oar most effective.

The instrument for burrowing, such as the Mole presents (fig. 2), is not very different in form and character

Fig. 2.



External form and skeleton of the fore-limb of the Mole (*Talpa Europæa*).

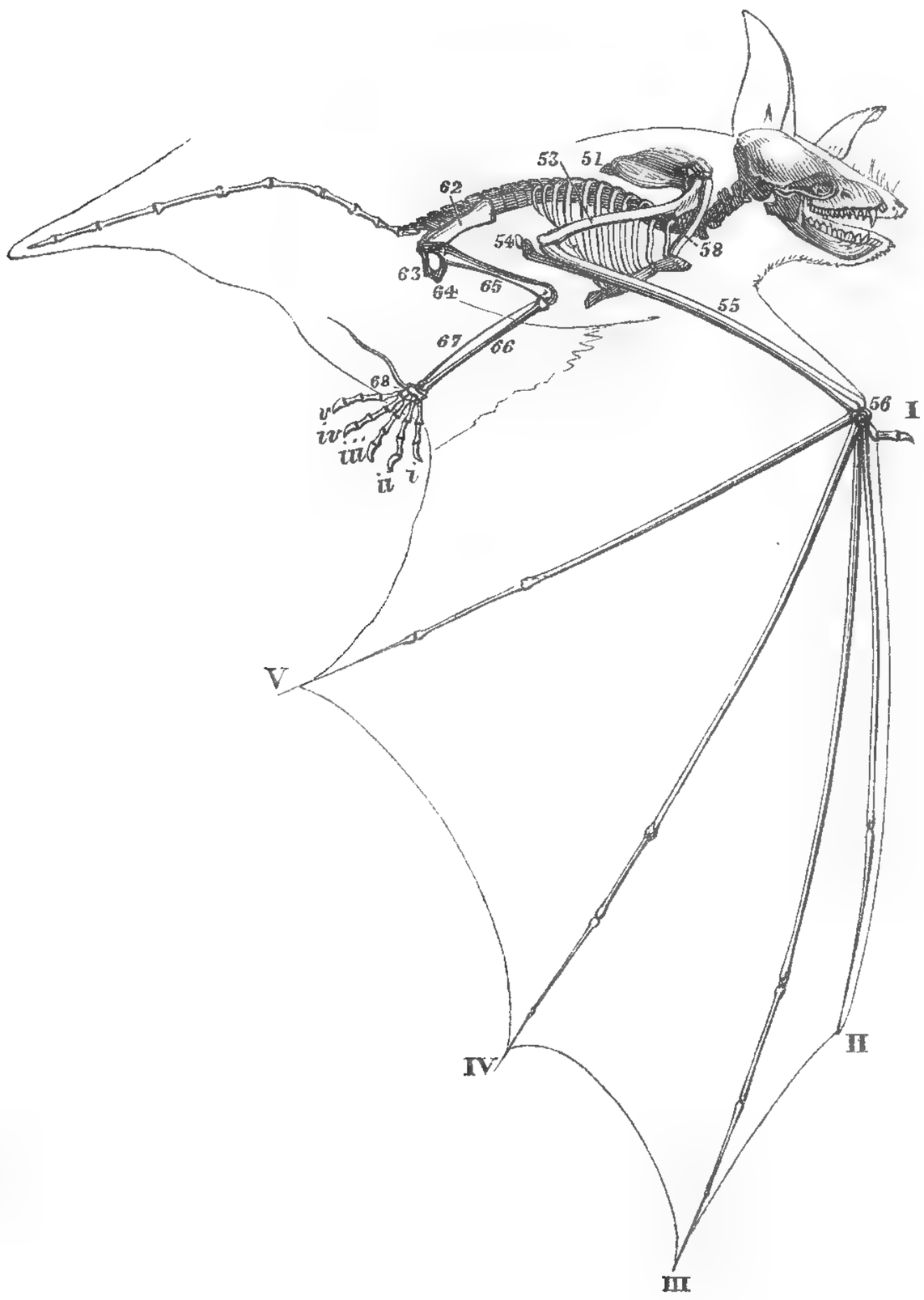
from the fin; but being destined to displace a denser element than water, it is shorter in proportion to its breadth, and much stronger: it resembles the fin in consisting, seemingly, of but one segment or joint, and being moveable as a whole only where it is set on to the trunk. The free border, however, instead of being smooth and thin, is notched, and armed with a row of hard, tooth-like, horny

were so denominated from a loose appreciation of this analogy, and convenience obviously suggests their retention in an arbitrary sense. To attempt to change the application of these names from a supposed more accurate appreciation of the analogical resemblance, argues either a mind more subservient to nomenclature than zealous for the advancement of the science of Nature; or an ignorance of the distinct systems to which the skeletons of the limbs of Articulates and Vertebrates owe their origin.

points, adapted for scraping and throwing back the soil. With such rapidity does the mole effect this purpose*, that it may literally be said to 'swim through the earth.'

The third form of limb or locomotive member here exhibited (fig. 3), offers a striking contrast to the burrowing

Fig. 3.



External form and skeleton of the wing of the Bat.

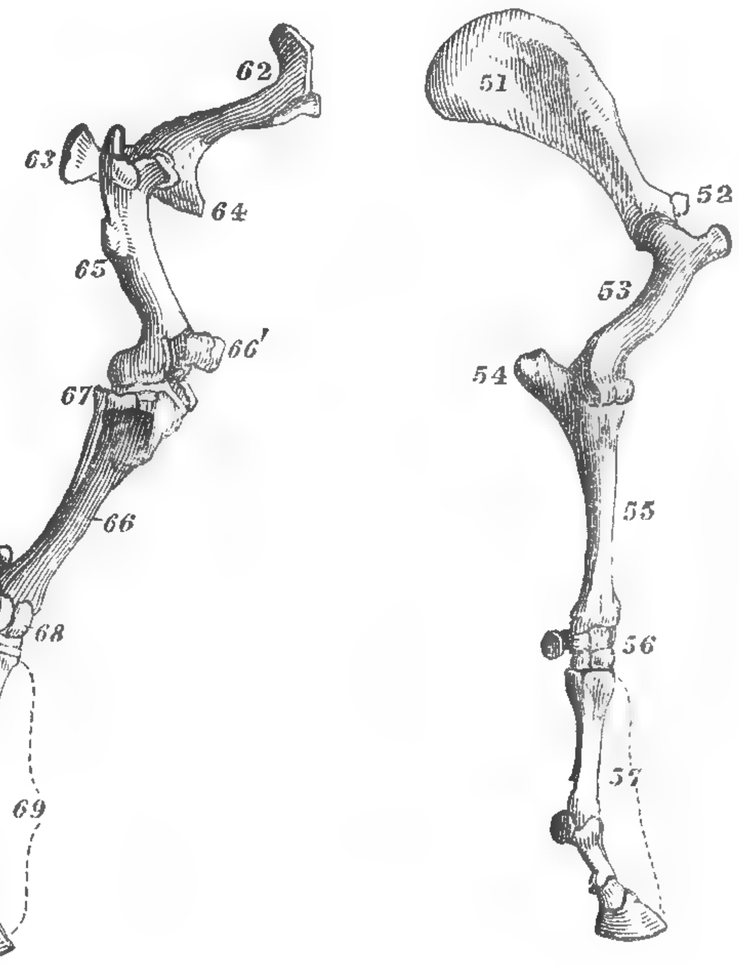
trowel we were last contemplating. It is a thin, vastly expanded sheet of membrane, sustained, like an umbrella, by slender rays, and flapped by means of these to and fro

* Prof. Bell, History of British Quadrupeds, p. 96, 8vo, Van Voorst.

in the air; and with such force and rapidity, as, combined with its extensive surface, to make it react upon the attenuated element more powerfully than gravitation can attract the weight to which the limb is attached, and consequently the body is raised aloft and moved swiftly through the air; in brief, the animal flies, and these instruments of its aërial course are called 'wings.'

When a quadruped has to move swiftly along the surface of the earth by reacting upon the hard ground, its limbs are as remarkable for their length and slenderness as those of the burrower or swimmer are for their shortness and breadth. In the racer the instruments of its rapid course are four long tapering columns, with joints permitting

Fig. 4.



Skeleton of the fore- and hind-leg of a Horse.

them to bend in opposite directions, and of the form represented in the diagram (fig. 4) and familiar to all: each column rests upon a slightly expanded base encased by the hard horny sheath which we call the 'hoof.'

When the limbs are adapted for grasping as well as running, they are divided at their extremities into move-

able appendages or digits, one of which can be opposed to the others and retain the object of their mutual pressure. Each of the four extremities is so organized in the ape and monkey, which are thus especially adapted for climbing and living in trees.

In Man the principle of special adaptation goes further; and, whilst one pair of limbs is expressly organized for locomotion and standing in the erect position, the other pair is left free to execute the manifold behests of his rational and inventive Will, and is exquisitely organized for delicate touch and prehension, emphatically called 'manipulation.'

Such are some of the more striking amongst the countless purposes to which the parts of animals called 'limbs' are adapted, and such the consequent diversity of their outward shapes and proportions. We cannot be surprised at this; it could not be otherwise: the instrument must be equal to its office. And consider the various devices that human ingenuity has conceived and human skill and perseverance have put into practice in order to obtain corresponding results!

To break his ocean-bounds the islander fabricates his craft, and glides over the water by means of the oar, the sail, or the paddle-wheel. To quit the dull earth Man inflates the balloon, and soars aloft, and, perhaps, endeavours to steer or guide his course by the action of broad expanded sheets, like wings. With the arched shield and the spade or pick he bores the tunnel: and his modes of accelerating his speed in moving over the surface of the ground are many and various. But by whatever means or instruments Man aids, or supersedes, his natural locomotive organs, such instruments are adapted expressly and immediately to the end proposed. He does not fetter himself by the trammels of any common type of locomotive instrument, and increase his pains by having to adjust the parts and compensate their proportions, so as best to perform

the end required without deviating from the pattern previously laid down for all. There is no community of plan or structure between the boat and the balloon, between Stephenson's locomotive engine and Brunel's tunnelling machinery: a very remote analogy, if any, can be traced between the instruments devised by man to travel in the air and on the sea, through the earth or along its surface.

Nor should we anticipate, if animated in our researches by the quest of final causes in the belief that they were the sole governing principle of organization, a much greater amount of conformity in the construction of the natural instruments by means of which those different elements are traversed by different animals. The teleologist would rather expect to find the same direct and purposive adaptation of the limb to its office as in the machine. A deep and pregnant principle in philosophy, therefore, is concerned in the issue of such dissections, and to these, therefore, I now pass, premising that the end in view will be attained without extending the comparison beyond the framework of the limbs, or the leverage of the bones and joints.

The human anatomist is of course familiar with this part of the skeleton in man. The arm is suspended from a broad bone called 'scapula' (Frontispiece, and Plate I. fig. 6, 51), and the shoulder-joint is strengthened by a slender bone called 'clavicle' (58), which abuts against the top of the 'sternum' (59), forming with its fellow an inverted arch, called in Comparative Anatomy the 'scapular arch.' The arm proper is appended to this arch: its first joint or segment is formed by a single long bone, the 'humerus' (53); its second joint, by a pair of shorter and more slender bones, the 'radius (55) and ulna' (54); and the hand or third segment is formed by a group of little thick bones, the 'carpals' (56), and by five rays or digits; one (I) consisting of three segments, the rest (II—V) of four segments each; the five bones joining the carpus being called 'metacarpals,' and the others the 'phalanges.'

When we proceed to compare with this the skeleton of the corresponding limb of the horse, ox, or other hoofed animal, the simplification of structure seems not to be in the ratio of the loss of function: almost all that the hoof can be made to do is to rest upon or beat against the ground; and yet we find in the solidungulate limb (fig. 4) the broad scapula (51), the long humerus (53), the radius (55) and ulna (54), the carpus (56), the metacarpus (57) and the digital phalanges. There is a diminution and simplification of accessory parts, but the essentials are maintained: it is obvious that the same type has governed the formation of the two limbs compared. The most marked distinction is the total absence of the clavicle in the hoofed quadruped: the shoulder-joint did not need to be made the fixed point upon which the fore-limb might rotate in a variety of directions; on the contrary, the movements of the humerus in the horse, though restricted almost to one plane, are extensive, and the scapula must play backwards and forwards to some extent with the limb; which movements would have been impeded had it been bound by a brittle bony bar to the sternum.

In like manner, since the hand had no need in the horse or ox to be turned, now prone now supine, in subserviency to manipulation, the accessory joints that allow the radius to rotate on the ulna are abolished, and the ulna is retained only in so far as it is required to strengthen the radius, make the joint of the elbow more secure, and give advantageous attachment to certain muscles. Here, however, we plainly see the same bone, with its olecranon (Frontispiece and fig. 4, 54), although it is anchylosed to the radius (55) and forms what, in Human anatomy, would be called a process of that bone.

The carpal series of small bones answers almost exactly, bone for bone, to that in man*: the hand of the horse,

* Compare fig. 6, *s*, l, *c*, p, *z*, *m*, *u*, with the carpal bones similarly lettered in the human skeleton, Pl. I. fig. 6, 56.

though to outward view reduced to a single digit, yet shows the rudiments of two others (fig. 6, II and V) when anatomized; these are called 'splint-bones' by the Veterinarians; but we shall presently demonstrate the very fingers in the human hand to which they answer.

If we had little *à-priori* ground to expect so much conformity between the skeleton of the arm of man and that of the fore-limb of the horse, still less have we to anticipate such between these and the bony frame of the wide-spread wing of the bat. Yet you perceive (fig. 3) that the essential similarity of its composition to that of the human arm (Frontispiece) is greater, the difference depending more on the proportion than on the change or suppression of parts.

Besides the scapula (51) we have the clavicle (58), which reappears in its perfect state; strong, long and curved, rendering the shoulder-joint a firm 'point d'appui' to the vigorous strokes of the wing that centre in the head of the humerus. This bone (53) is proportionally as long as in man, but the bones of the fore-arm are much longer, at least the radius (55); for, rotatory movement of the wrist being here as little needed as in the horse, the ulna (54) is similarly atrophied and reduced to its olecranon and proximal half which is anchylosed to the radius. The small bones of the wrist or carpus (56) again succeed the radius, and here they support the same number of fingers as in man, of which, also, the first or innermost (I) is distinguished from the rest (II—V) by its shortness and difference of direction, and by its inferior number of phalanges. The chief modification of the bones of the fore-limb in the bat consists in the extreme elongation and attenuation of the four ordinary fingers; two or more of which consist, as in man, of the metacarpal bone and of three phalanges, proximal, middle and distal; but the last phalanx tapers to a point and is without a nail.

To skim the air and to burrow in the earth would seem

to require instruments as different in construction as in size and shape; but observe how closely the skeleton of the mole's trowel (fig. 2) conforms in the number and relative position of the parts to that of the bat's wing! The chief change is in this,—whatever is elongated and attenuated in the bat is shortened and thickened in the mole. With regard to one bone, indeed, the statement may be reversed, for the scapula (fig. 2, 51) now appears as a long, straight, prismatic column, and is the centre of a most powerful mass of muscle in the recent limb. The clavicle (58) on the other hand, though perfect, is a short thick cube: the humerus (53) must be classed by its shape amongst the broad bones, the ordinary form of this bone and the scapula being reversed in the mole. The radius (55) and ulna (54) are both completely developed, and enjoy all the accessory rotatory movements as in man; but are relatively much more powerful bones, especially the ulna, which has an enormous olecranon as the fulcrum of powerful muscular forces. Then follow, as usual, the double series of little carpal bones (56), supporting five digits (I—V), which, notwithstanding they are buried up to the claws in a sheath of tough skin, have precisely the same number of bones and joints as in the prehensile hand of man; only that every bone, save the last in each digit, is as broad and thick as it is long. The chief deviation from the human type is by redundancy instead of deficiency, and is exemplified by one or two supernumerary carpal ossicles, the most remarkable of which is sabre-shaped (56′), and strengthens the digging or scraping edge of the broad palm.

If the dissector were little prepared on teleological grounds to meet with the full number of joints or segments in the short and seemingly simple trowel of the mole, he could still less expect to find them hidden beneath the common undivided sheath of the fin of the dugong or whale. Yet the bones of this simple form of limb

offer perhaps the most striking and suggestive instance of an adherence to type, necessitated as it would seem, notwithstanding the absence of all those movements and appliances of the limb that explain the presence of the several segments, on the principle of final causes, in the horse and man.

First we have the blade-bone or scapula (fig. 1, 51), now again broad and flat; next the single arm-bone (53), this united by an elbow-joint to a radius (55) and ulna (54); the latter complete with its elbow-prominence or olecranon: the two antibrachial bones are followed by the ossicles of the carpus (56) in their normal double series, and these support the five digits (I–V), with the first distinguished from the rest by its inferior number of phalanges.

In descending to an inferior aquatic species and examining the corresponding (pectoral) fin of a fish (Pl. I. fig. 2), we find indeed one segment (53) of the limb abrogated, and its framework attached to the scapular arch (51, 52) by the two bones answering to radius (55) and ulna (54); these, however, are followed by the constant carpals (56), which support a variable number of digits (57, *a*) in the form of slender pointed rays, like those in the bat, but usually more numerous, often bifurcated, and always divided into a greater number of segments. We clearly recognise, however, the hand, the wrist and the fore-arm in this fish's fin. The number of digital rays in some fishes falls short of the typical 5, and in the *Lepidosiren* (Pl. I. fig. 7) they are reduced to 1, which is partially divided into many segments, and in which all distinction of arm, fore-arm and hand is lost. In the *Muræna* and *Anguis* the scapular arch alone remains, the appended limb being lost; and lastly, in ordinary Serpents and Cyclostomous fishes (Lampreys) all trace of both arch and appendage has vanished.

On glancing back over the great classes of animals represented by the examples that have been adduced, we perceive within what narrow limits of the Vertebrate series

the type of the anterior or pectoral member, as shown in man, ceases to be recognizable; and then, not by a change, but by a fading away of the pattern, as the limb rapidly disappears at the extreme of the series. It is by the study of these transitory or rudimental manifestations of the limbs that we gain the deepest and truest insight into their essential nature. But before proceeding to this part of my inquiry, I shall advert to another class of correspondences or evidences of unity of type which give additional impulse to the pursuit of the higher generalization that may reveal the meaning of those evidences.

The bilateral symmetry of the body and the consequent answerableness or parallelism of the parts or organs of one side to those of another, are too obvious facts to need more than a passing reference. They have been universally recognized, were scientifically enunciated by the Father of Natural History*, and in all languages the parts are designated by the same names, and distinguished only by the epithets 'right' and 'left.' Thus we have a right arm and a left arm, a right leg and a left leg, and so with respect to their several segments and the subdivisions of these, down to the right thumb and the left thumb, the right great-toe and the left great-toe, &c. The identity of structure in this transverse direction is complete. The great Newton was so much struck by the contemplation of this law of symmetry, that he breaks out into the following emphatic and beautiful anticipation of the aim and general result of Philosophical Anatomy:—"Tam miram uniformitatem in planetarum systemate, necessario fatendum est intelligentia et consilio fuisse effectam! Idemque dici possit de uniformitate illa quæ est in corporibus animalium. Habent videlicet animalia pleraque omnia, bina latera, dextrum et sinistrum,

* "Habet autem homo partes superas et inferas; anteriores et posteriores; dextras et sinistras. Dextræ igitur atque sinistræ partes omnes inter se similes fere et eædem, præterquam quod sinistræ imbecilliores." *Schneider's Aristotelis de Animal. Hist. Lib.* II., tom. ii. p. 30.

forma consimili: et in lateribus illis, a posteriore quidem corporis sui parte, pedes binos; ab anteriori autem parte, binos armos, vel pedes, vel alas, humeris affixos: interque humeros collum in spinam excurrens, cui affixum est caput; in eoque capite binas aures, binos oculos, nasum, os et linguam; similiter posita omnia, in omnibus fere animalibus."—*Newton, Optices*, 1719, p. 411. Aristotle, also, saw that, besides the lateral symmetry, the inferior parts corresponded in a certain proportion to the superior parts.

The most superficial comparison of the limbs of our own species must impress the observer with the resemblance between the arm and the leg in their general form and character, notwithstanding the marked contrast of their powers and offices which characterizes the human species. Every one may see that the thigh answers to the arm proper, the leg to the fore-arm, the ankle to the wrist, the five-toed foot to the five-fingered hand, in which also the thick thumb may be recognized as answering to the great-toe, and the little finger to the little toe, and so of the rest.

When we proceed to the comparison of the bones of the two limbs, the correspondence becomes more striking. A broad and flat bone, the haunch-bone or 'ilium' (Frontispiece and Pl. I. fig. 6, 62), with its base towards the spine and its apex forming the hip-joint, plainly repeats the scapula (51), and the inverted arch is completed by the meeting of two broad and perforated plates below (63 & 64), which in a general way correspond with the clavicles. The single bone of the thigh (65) more decidedly repeats the single bone of the arm (53)*; the two bones of the leg

* It will, of course, be obvious that the humerus is not 'the same bone' as the femur of the same individual in the same sense in which the humerus of one individual or species is said to be 'the same bone' as the humerus of another individual or species. In the instance of serial homology above-cited, the femur, though repeating in its segment the humerus in the more advanced segment, is not its namesake or

(tibia, 56, and fibula, 57) repeat the two bones of the fore-arm (radius, 55, and ulna, 54); the small thick bones of the tarsus (68) those of the carpus (56); the five metatarsals the five metacarpals: and, if proof were wanting of the serial homology, as I have termed these relations, between the thumb (1) and great toe (*i*), we find it in the skeleton, which shows that both have only two phalanges, whilst the remaining four toes, notwithstanding most of them are shorter than the great-toe, have the same superior number of phalanges, viz. three, as the four fingers have on the hand. The bones that are developed in tendons, which glide over joints, in order to remove them from the centre of motion, are the least regular or subject to type: they are called 'sesamoids,' and the largest and most conspicuous of these is that of the knee-pan or 'patella' (66′), to which there is no corresponding ossification in the homotypal tendon of the arm.

In comparing the bones of the hind-leg (fig. 4, B) with those of the fore-leg (fig. 4, A) of the horse, we find that the modifications by which the latter depart from the type of the skeleton of the human arm are repeated both in kind and degree in the hind-leg. The foot is similarly simplified, attenuated and elongated: it consists chiefly of a single toe (*iii*), with the same number of joints as that of the fore-foot, and touches the ground by a single hoof: rudiments of two other toes (*ii* and *iv*, fig. 19, Pl. I.) are similarly represented by the splint-bones: there is a group of tarsal bones (fig. 4, 68) answering to the carpal ones (*ib.* 56). The segment of the leg is formed chiefly by a single bone (66), like the corresponding segment of the fore-limb (53); the

'homologue.' I have proposed, therefore, to call the bones so related serially in the same skeleton 'homotypes,' and to restrict the term 'homologue' to the corresponding bones in different individuals or species, which bones bear, or ought to bear, the same names. See 'On the Archetype and Homologies of the Vertebrate Skeleton.' 8vo, V. Voorst, 1848.

fibula (67) being reduced to a rudiment of its upper end, as the ulna (54) is in the antibrachium. The short oblique femur (65) repeats the short oblique humerus (53), only the obliquity is in the opposite sense; but the modification of the end of the bone which produces this change is feeble in comparison to that of the entire femur in different species: compare *e. g.* the femur in man and the megatherium. The long and narrow ilium (62) departs from the human type of that bone just as the long and narrow scapula (51) does from its homologue in man; the chief difference that will be noticed is, that, whereas the coracoid (52) is rudimental and the clavicle *nil* in the fore-limb, their homotypes the ischium (63) and pubis (64) are fully developed, and complete the arch to which the hind-limb is attached. When we remember that the hind-limbs are the chief instruments in propelling the body, we shall see the necessity for the firm and unyielding condition of the part that immediately receives the impetus from the thigh-bone and transmits it to the trunk.

The scapular arch is the seat of more variety in regard to its closed or open state in the class Mammalia than in the lower Vertebrata, which depart less from the type in retaining its complete or closed state. But what chiefly concerns us in the present parallelism between the fore and hind limbs is the fact that the pelvic arch is subject in certain mammals to the same variety by defect as the scapular arch is. Thus, in the skeleton of the bat (fig. 3), in which we saw the scapular arch completed by the extension of the strong clavicles (58) to the sternum, the pelvic arch remains open below, the pubis (64) and ischium (63) being rudimental and forming mere 'processes' of the ilium (62), as the coracoid does of the scapula. Here, therefore, the supporting arches of the fore- and hind-limbs present the reverse conditions to those in the horse in regard to their completeness, and the final cause is obvious. In the bat the fore-limbs are the locomotive instruments, the hind-limbs

merely the supporting members from which the animal suspends itself, head downwards.

But if we find that the correspondence between the scapular and pelvic arches is interrupted in the bat to the same extent as in the horse, though contrariwise, the pelvis being open and the scapular arch closed, in relation to the different values of their respective limbs in locomotion; yet the parallelism between the fore- and hind-limbs themselves is equally complete as to their composition. The single femur (65) answers to the humerus (53), and the tibia (66) alone is fully developed in the leg, as the radius (55) is in the fore-arm: whilst the fibula (67) exhibits an equally rudimental and incomplete state to that presented by the ulna (54); only in the leg the lower half of the bone is retained, whilst in the arm it is the upper half: and we may observe a similar contrast in the Camel-tribe. The tarsus (68) in the bat again parallels the carpus (56), and the digits are developed in the same typical number in the foot as in the hand, only that they retain their more normal form and unguiculate character.

There is one item of conformity of structure between the fore- and hind-limbs of certain bats not usually met with in other animals, viz. the development of a sesamoid in the tendon of the *biceps brachii* in front of the elbow-joint, which is the true homotype of the patella in the leg. There is also a second sesamoid above the olecranon (54) of the bat, which has been thought to represent the patella; but I shall presently advert to the true homotype of the ulnar sesamoid in the hind-limb.

The comparison between the fore- and hind-limbs in the mole may be briefly discussed, as they differ in their proportions, not in their composition.

The pelvic arch is reduced in its transverse dimensions to the ordinary size of the hæmal arches in the tail, and surrounds only the pelvic continuation of the aortic arterial trunk; but the ilium resembles the scapula in its

length and slenderness: the femur—the homotype of the humerus—is followed by a complete tibia and fibula, answering to the complete radius and ulna in the fore-limb: there is a tarsal segment of small ossicles answering to the carpal series, and five toes with the same number of joints as those of the fore-foot, the first or innermost of each having but two phalanges.

We cannot pursue this parallelism in respect of the limbs that have been adduced as examples of the fin or organ of swimming (fig. 1), because all the whale-tribe are characterized by the absence of the ventral fins or representatives of the hind-legs. We find however on dissection, as in the case of the *Muræna* and slow-worm (*Anguis*), that traces of their sustaining arch still exist. In the whale the ischium or inferior member of the arch is present: in the dugong there is both a rudimental ischium and ilium.

The Reptilian sea-turtle (*Chelone*) is an instance in which both fore- and hind-limbs are modified to serve as fins; but I have selected in illustration of this comparison an extinct form of Reptile, which of all the ancient Sea-lizards (*Enaliosauria*) was most nearly allied to the *Chelonia*. The skeleton of the *Plesiosaurus* (Pl. II.) shows the unity of type closely preserved between the fore- and hind-limbs.

The scapula (51) is a long, narrow, almost vertical bone, both in shape and position like a rib: the arch is completed below by a broad coracoid (52) and a clavicle (58). The ilium (62) in like manner retains much of its proper pleurapophysial or rib-like character, and the pelvic arch is completed below by a broad ischium (63) and pubis (64). The flattened femur (65) closely parallels the flattened humerus (53). In the two short bones of the next segment, the stronger and straighter one in the pectoral fin (55) obviously represents the radius, and its homotype the tibia (66) has the same shape in the ventral fin. The ulna (54)

is shorter than the radius, is curved and projects backwards; the fibula (67) repeats the same character: there is a carpal group of ossicles (56) and a tarsal group of ossicles (68); a row of five metacarpals (57), and a row of five metatarsals (69); and the number of the digits, as well as the number of their joints respectively, is almost identical in both fore- and hind-paddles.

The conformity is the more striking here, because it is not broken by the opposite flexures that characterise the corresponding segments of the fore- and hind-limbs in the terrestrial mammalia; and it is the more interesting and significative as being manifested by an animal which lived and died at a period so remote as the existence of that ocean from which the lias of Somersetshire was precipitated.

Vicq-d'Azyr seems to have been the first anatomist whose attention was so much awakened by the perception of these serial correspondences, at least in the human frame, as to have led him to pursue them in detail. He communicated the result of his comparisons to the Parisian Academy, in whose celebrated 'Mémoires' it appears in the year 1774, under the title "Parallèle des Os que composent les Extrémités." The philosophic Condorcet, at that time Perpetual Secretary to the Academy, was so much struck by the grand views of animal structures which this mode of inquiry promised to disclose, that in his Report on the Memoir he characterises it as 'a new kind of Comparative Anatomy.' It seldom happens, however, in such early excursions into a foreign territory, that success is complete; and Vicq-d'Azyr, though right in respect of the scapula, humerus, and bones of the hand, was led astray by the different proportions of the ulna and fibula in the human skeleton in his comparison of those bones.

Preconceptions from modifications of *form* can only be corrected by an extended survey of such variable morphological characters. Vicq-d'Azyr conceived that the ante-

rior extremity was not paralleled or repeated by the posterior one of its own side, but by that of the opposite side; the right arm by the left leg, and *vice versâ*; and Cuvier adopted this notion of a dextro-sinistral conformity*.

Vicq-d'Azyr also supposed that the ulna in the fore-arm was the correspondent of the tibia in the leg, with the patella as the detached olecranon, and that the radius answered to the fibula; a mistake which he could scarcely have fallen into had he extended his comparisons to the lower Mammalia, or known the instances which I shall presently adduce from the Marsupial order.

So tardily however have the exact generalizations of Philosophic Anatomy been appreciated in France, that, in one of the latest and most elaborate 'Manuals of Descriptive Anatomy,'—a work of considerable repute for its minute accuracy of detail,—it is laid down, that "the upper end of the tibia is represented by the upper half of the ulna, and the lower half of the tibia by the lower half of the radius; whilst the fibula is represented by the upper half of the radius and the lower half of the ulna†."

Nature, however, when rightly interrogated and propitiated by due observant service, extricates us from these complex involutions and alternations of serial homology, and makes the simple truth plain. The extensive knowledge of Comparative Anatomy possessed by my revered preceptor in Anatomy, Dr. Barclay, enabled him truly to interpret the parallelism of the bones of the fore-arm and of the leg-proper. He showed how the ulna and its homotype the fibula exhibited the same 'variety and unsteadiness of character, sometimes large, sometimes small,

* Leçons d'Anat. Comp. t. i. 1836, p. 342.

† "L'extrémité supérieure du tibia est représentée par la moitié supérieure du cubitus, et la moitié inférieure du tibia par la moitié inférieure du radius; tandis que le péroné est représenté par la moitié supérieure du radius et par la moitié inférieure du cubitus."—*Cruvelhier, Anatomie Déscriptive*, t. i. p. 315.

and sometimes merely a process' of the more constant bone of their respective segments*.

Some anatomists may still be biased by the cause of Vicq-d'Azyr's mistake, viz. the great development of the olecranon or upper end of the ulna: but it needs only instances in which the fibula manifests a similar development to satisfy the most sceptical as to the soundness of the grounds on which the Homological conclusions illustrated in Plate I. figs. 15 and 16 are based. The marsupial and monotrematous animals are fertile in this parallel instance of excessive development. The head of the fibula in the ornithorhynchus extends far beyond the knee-joint, and is expanded like the olecranon in the mole's ulna. Many of the marsupial quadrupeds have a rotatory motion of the hind-foot analogous to the pronation and supination of the hand: in the opossums and phalangers the great-toe is an opposable thumb, whilst its homotype in the hand remains parallel with the other fingers, and the location of the foot and hand is thus the reverse of that in the human subject: whence naturalists have styled these marsupial animals '*Pedimana*'—foot-handed. One might expect that the modifications of the

* M. Flourens had probably never seen Dr. Barclay's 'Explanations of Mitchel's Plates of the Bones,' 4to, 1824, when he wrote, "Il a été plus difficile de rapporter individuellement chaque os d'un membre à chaque os de l'autre. Chose étrange, on ne sait pas encore s'il faut comparer ensemble l'*humerus* et le *femur* du même côté ou l'*humerus* d'un côté et le *femur* de l'autre; on ne sait pas quel est celui des deux os de l'*avant-bras*, le *radius* ou le *cubitus*, qu'il faut comparer à tel ou tel des deux os de la jambe, le *tibia* ou le *péroné*." He supports his reproduction of Barclay's proposition regarding the serial homology of the bones of the fore-arm and leg by similar remarks drawn from Comparative Anatomy. "Déjà," writes M. Flourens, "dans les Chauve-souris, dans les *Galéopithèques*, le *cubitus* n'est plus qu'un filet très grèle; ce même *cubitus* ne se montre plus qu'en vestige dans les *Ruminans*, dans les *Solipèdes*; le *péroné*, déjà très grèle dans les Chauve-souris, déjà simple rudiment styloïde dans le *Cheval*, manque à-peu-près tout-à-fait dans plusieurs *Ruminans*."—*Annales des Sciences Naturelles*, 1838, pp. 35, 37.

bones of the leg, in subserviency to those transferred powers of prehension, would resemble the characters that disguise the serial homology of the bones of the fore-arm in man; and accordingly we find that, whilst the co-adapted joints between the tibia and fibula in the *Pedimana* are such as to permit their reciprocal rotation, the proximal end of the fibula is developed to afford the requisite advantage to the muscles acting upon the foot.

In illustration of this instructive parallelism I have selected the leg-bones of the wombat (*Phascolomys*, Pl. I. figs. 15 and 16), because in them not only does the fibula (67) show the broad, flat and high process from its proximal end, but also a superadded sesamoid (67′) which parallels the peculiarity observable in the olecranon of the bat (fig. 3, 54), viz. the separate superincumbent ossicle, which at first sight might have been deemed confirmatory of V.-d'Azyr's idea of the patella being a detached olecranon.

In instituting the same kind of comparison between the little bones of the carpus and tarsus, I have been forcibly struck with the perspicacity with which V.-d'Azyr detected their true homologies in the human skeleton, notwithstanding their difference in form and number. He compares the 'scaphoides' (*sc*) of the wrist (Pl. I. fig. 6, 56) with the 'scaphoides' or 'naviculare' (*s*) of the ankle (*ib.* 68), the 'lunare' (*l*) with the 'astragalus' (*a*), the 'cuneiforme' (*cn*) and 'pisiforme' (*p*), together, with the 'calcaneum' (*cl, cl*); and, in the second row, the 'trapezium' (*t*) with the 'entocuneiforme' (*ci*), the 'trapezoïdes' (*z*) with the 'mesocuneiforme' (*cm*), the 'os magnum' (*m*) with the 'ectocuneiforme' (*ce*), and the 'unciforme' (*u*) with the 'cuboïdes' (*b*).

To some anthropotomists, viewing the different position of the scaphoid in the wrist (*sc*) and ankle (*s*) of the human skeleton (Pl. I. fig. 6), these comparisons may still seem forced and fanciful: and since the calcaneum (*cl, cl*) is actually developed from a single ossific centre, they may regard its division as purely arbitrary, in order to form the homotypes

of the two outer bones of the proximal row of carpal bones. And these objections can only be explained and removed by reference to an enlarged survey of all the modifications of the bones in question.

As M. Flourens, in adopting the determinations of Vicq-d'Azyr, has not met these obvious and seemingly natural objections, by reference to Comparative Anatomy, I shall adduce some of those instances which illustrate the true character of the carpal and tarsal bones, especially in regard to the classification of the bones of the skeleton into 'simple' and 'compound*.'

Without looking further than the human skeleton, it will be obvious that the distal row of the tarsal bones is undisturbed (Pl. I. fig. 6, *ci*, *cm*, *ce*, *b*), and in the same relation to the metatarsals as the distal row of the carpals (*t*, *z*, *m*, *u*) is to the metacarpals: the cuboid (*b*) for example supports the two outer toes, as the unciforme (*u*) supports the two outer fingers. But the same order does not prevail in the arrangement of the other bones of the tarsus: the scaphoid (*s*) is so displaced as to represent part of an intermediate row. M. Flourens explains this modification by reference to the necessity of the greater length required by the inner digit of the foot for the functions of that member, which elongation he affirms to be exclusively caused by this displacement of the scaphoid†. A glance, however, at the relations of the advanced scaphoid in the human skeleton (*s* in fig. 6, Pl. I.) will show that it ought equally to affect the length of the toes attached to the

* 'On the Archetype and Homologies of the Skeleton,' 8vo, pp. 103–105.

† "Or, supposez le *semilunaire* grandi à la main, comme l'*astragale* l'est au pied, il repoussera nécessairement le *scaphoïde*, il le portera en avant; et, ce qui le prouve, c'est l'allongement du pouce du pied, comparé au pouce de la main, allongement qui n'a, en effet, d'autre cause que le déplacement du *scaphoïde*, son transport en avant, et sa position sur la même ligne que les autres os du pouce."—*Annales des Sciences Naturelles*, t. x. p. 39, 1838.

mesocuneiform (*cm*) and ectocuneiform (*ce*) bones; and that the elongation of the great-toe is due rather to the disproportionate length of the entocuneiform (*ci*) or homotype of the little trapezium (*t*) of the wrist. The true explanation, therefore, of the difference in question must be sought for in other and wider considerations.

I have elsewhere remarked* that, "In mammalian quadrupeds generally the fore-limb takes the greater share in the support, the hind-limb in the propulsion of the body. The *manus* is accordingly commonly shorter and broader than the *pes*; this may be seen in the terminal segment of even the monodactyle hand and foot of the horse. Consequently the transverse direction prevails in the arrangement of the carpal bones and the longitudinal in that of the tarsal bones. The difference is least in the carpus and tarsus of the long and slender fore- and hind-hands of the Quadrumana. If the carpus of the chimpanzee, for example, be compared with that of man, the first difference which presents itself is the comparatively small proportion of the scaphoid which articulates with the radius, as compared with that in man, in whom the distal articulation of the radius (Pl. I. fig. 6, 55) is equally divided between the scaphoides (*sc*) and lunare (*l*) which are on the same parallel transverse series. In the orang (Pl. I. fig. 13), the divided scaphoid (*s*, *s'*) extends, almost as much from the lunare as from the radius, along the radial side of the carpus, to reach the trapezium (*t*) and trapezoides (*z*); it is in great part interposed between the lunare (*l*) of the proximal row and the trapezium and trapezoid of the distal row of the carpal bones. The similarity of its connections, therefore, in the carpus with those of the scaphoid in the tarsus (Pl. I. fig. 14, *s*) is so close that the serial homology of the two bones is unmistakeable. The astragalus (*ib. a*), then, in the foot, repeats the os lunare (*l*) in the hand, but usurps the whole of the articular surface of

* 'On the Archetype and Homologies of the Skeleton,' p. 167.

the tibia, and presents a larger proportional size, especially in man, whose erect position required such exaggerated development of the astragalus, or homotype of the lunare. The prominent part of the calcaneum (Pl. I. figs. 6 and 14, *cl'*) obviously repeats the prominent pisiforme (figs. 6 and 13, *p*), and the body of the calcaneum (figs. 6 and 14, *cl*) articulates with the fibula, as the cuneiforme (figs. 6 and 13, *cu*) articulates with the ulna. The strain upon the homotype of the pisiforme (*cl'*) to produce the required effect in raising the back-part of the foot with its superincumbent weight upon the resisting ends of the toes, required its firm coalescence with the homotype of the cuneiforme." The calcaneum, therefore, is essentially a 'compound bone'; that is, it answers to two bones, and includes them ideally, though they be connate*. We might infer the same in respect to the unciform (*v*) in the hand and the cuboid (*b*) in the foot, seeing that they each support two digits, whilst the other ossicles of their series respectively support a single digit.

The test of the truth of this idea will be the result of a comparative survey of the carpal and tarsal bones in the Vertebrate series: and, accordingly, in descending to the cold-blooded animals that are more obedient to the archetypal law, and where more of the primitive ossific centres continue distinct, we find in the Chelonian reptiles for example (Pl. I. fig. 12) the unciform bone represented by two bones (*u*, *u'*), and each of the five metacarpals is supported by its own carpal ossicle. This structure naturally suggests that the normal or typical number of carpal bones is ten, viz. five in each row, corresponding with the typical number of the digits. But we should search in vain the

* This term is used in the definite sense explained in my work on the 'Archetype of the Vertebrate Skeleton' (8vo, V. Voorst, p. 49), as signifying those essentially different parts which are not physically distinct at any stage of development; and in contradistinction to the term 'confluent,' which applies to those united parts which were originally distinct.

human carpus to find any characters that would justify our choice of the compound or essentially double bone in the proximal series, like those that indicate the compound bone in the distal series. Comparative Anatomy, however, affords the key to this problem and directs our choice. The same instance (Pl. I. fig. 12) which gives the typical bipartite condition of the unciforme (*u*, *u'*) also presents it in the 'scaphoïdes' (*s*, *s'*): and we become assured that the second ossicle (*s'*) is no mere accidental and exceptional supernumerary from the frequent repetition of the divided 'scaphoid' in higher classes: it reappears, for example, in the Quadrumana, and the typical character of the bone is even retained in the species which approaches so near to man as the orang-utan (Pl. I. fig. 13, *s*, *s'*). The only difference from the tortoise being, that whereas in that reptile the two scaphoids in the wrist articulate with the three carpal bones of the second row, answering to the three cuneiform bones of the ankle, and thus repeat the connections of the undivided tarsal 'scaphoid'—in the orang the divided carpal 'scaphoid' supports only the trapezium and trapezoïdes, answering to the inner and middle cuneiform bones, the os magnum (*m*) being so elongated as directly to articulate with the lunare (*l*). In both the tortoise and orang, however, we perceive that the arrangement of the five bones of the proximal row of the carpus is irregular, and parallels that of the corresponding bones of the tarsus; the two bones represented by the scaphoid intervening between the distal row and those bones that remain in the proximal row.

With what new interest must the human anatomist view the little ossicles of the carpus and tarsus when their homologies have been thus determined! It must be evident to him that their true nature could never have been understood by the study of them in the human skeleton alone, however minutely scrutinized there. But by the light reflected from Comparative Anatomy he is now en-

abled both to discern their homotypal relations and their natural classification. In the carpus, the lunare, cuneiforme, pisiforme, trapezium, trapezoïdes, and os magnum rank with the 'simple' bones; and the scaphoïdes and unciforme with the 'compound' bones. And so likewise in the tarsus, the calcaneum and cuboïdes are the compound bones, the others are simple bones. Connation or blending together of two essentially distinct bones is by no means however confined to the scaphoid and unciforme in the wrist, or to the calcaneum and cuboid in the ankle.

In many ferine, rodent, and marsupial quadrupeds the scaphoid unites with the lunare; examples of such scapho-lunar bone are shown in Pl. I. figs. 5 and 15, *sc*, *l*. In the sloth and megatherium the trapezium blends with the scaphoid. In the tarsus of the ruminants the cuboid is anchylosed to the scaphoid: an example of this scapho-cuboid bone is given in the hind-foot of the ox (*s*, *b*, fig. 18, Pl. I.), and other instances might be multiplied. Those that have been adduced may serve, however, to remind the hesitating or sceptical anatomist, that the same reasons which prevailed with Cuvier to recognise the compound character of the scapho-lunar bone of the lion, the scapho-trapezial bone of the sloth, and the scapho-cuboid bone of the ox, have led me to the same conclusion with regard to the unciforme in the carpus, the calcaneum in the tarsus, and the bone called scaphoid in both those segments of the limbs of man.

Another important and instructive result of the foregoing comparisons is the constancy of the relations of the distal series of carpal and tarsal bones, whether simple or compound, with the five digits with which they essentially correspond in number: for by this constancy of connexion we are able to determine the precise digits that are lost and retained when their number falls below the typical 5; to point out, for example, the finger in the hand of man that answers to the fore-foot of the horse, and the

toe that corresponds to its hind-foot; nay, the very nail in the hand or foot which becomes by excess of development the great hoof of the horse. Were anything wanting to impress the thinking mind with the conviction of the unity of type which pervades animal structures, it might be such a fact as this.

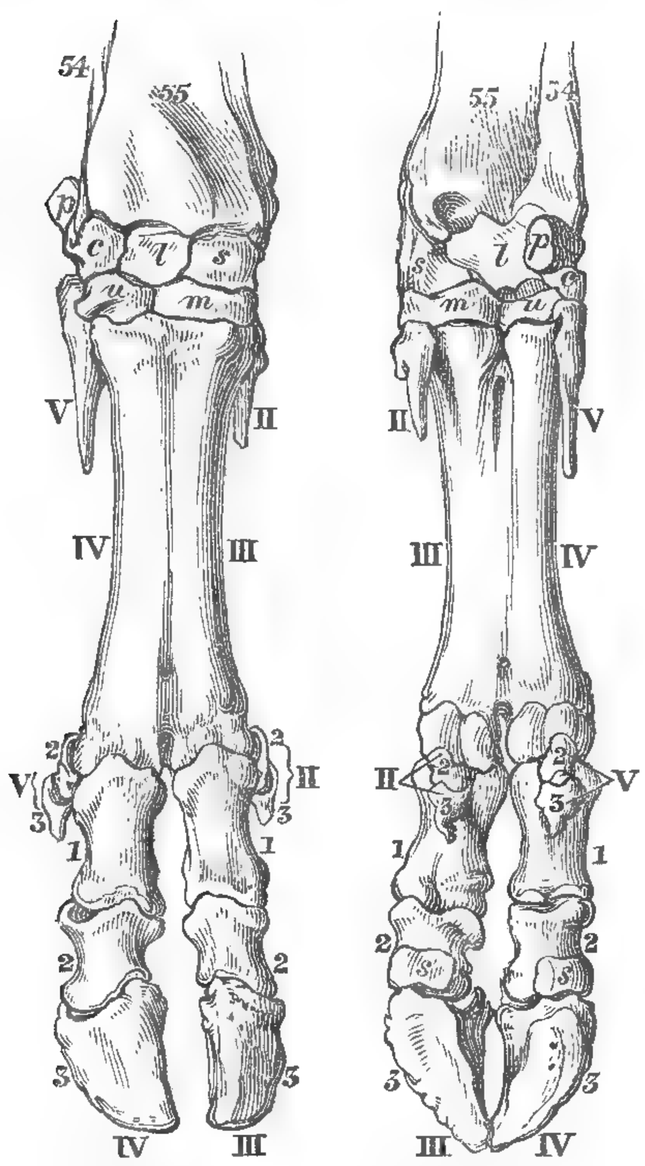
The small styliform ossicle which is attached to the trapezium in the wrist of the spider-monkey (*Ateles*) or the hyæna, is plainly shown by that connexion, besides its relations to the other digits, to be a remnant of the thumb—the first digit of the hand that disappears in the process of reduction. The similar ossicle that is attached to the diminished unciforme of the marsupial bandicoot, in like manner is shown by that connexion to be the rudiment of the little finger; the three remaining digits also retaining respectively their normal connexions with the trapezoïdes, the magnum, and the unciforme.

In the tridactyle rhinoceros a mere rudiment of the trapezium lingers in the wrist, but the homologue of the thumb is lost; and the part of the compound unciforme supporting the little finger has disappeared with every trace of that digit.

In the ox we find a rudiment of the fifth digit (fig. 5, v) attached to the outer part of the carpal bone (*u*) articulating with the outer half of the cannon-bone (IV); and thus we recognize the os unciforme supporting, besides that rudiment (v), the metacarpal of the fourth digit (IV), which has coalesced with that of the third digit (III): the inner half of the cannon-bone, representing the third or middle metacarpal, articulates, in fact, with a distinct carpal ossicle (*m*), which, by its relations to the unciforme (*u*) externally and to the lunare (*l*) and scaphoïdes (*s*) above, is plainly the homologue of the os magnum (*m*). A rudiment of the second metacarpal (II) is retained on the inner side of the base of the cannon-bone, and a trapezoid is distinct in the carpus of the camels and the diminutive

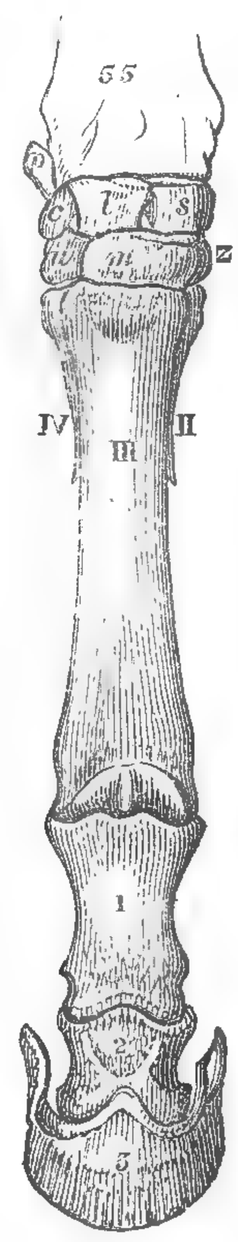
chevrotains (*Tragulus*); but it has coalesced with the magnum in the ox, and both trapezium and thumb have disappeared in all Ruminants. Thus we learn that the fully developed digits that support the cloven hoof of the Ruminants answer in the fore-foot to the middle and ring fingers of our hand, and that the cannon-bone consists of the coalesced metacarpals of those two fingers.

Fig. 5.



Bones of the fore-foot of the *Bos Urus*.

Fig. 6.



Bones of the fore-foot of the Horse.

When we examine the bones of the fore-foot of the horse (fig. 6), we find the cannon-bone (III) articulated to a single bone of the carpus (*m*), which, from its relations to the scaphoid (*s*) and lunare (*l*), is the homologue of the os magnum in the ox; but it is relatively of larger size, having increased to the dimensions required for its application to the whole of the proximal surface of the great metacarpal (III). This is not, however, the equivalent of

the two united bones (fig. 5, III and IV) so placed in the ruminant, for the unciforme (fig. 6, *u*) exists external to it, but reduced in size in conformity with the reduction of the rudimental metacarpal (IV) which it now supports. The carpus of the horse, in fact, resembles that of the rhinoceros more than that of the ox; and the readiest key to the nature and homologies of the bones of the horse's foot is afforded by comparison with that of the ponderous three-toed Pachyderm. The rudiment of the trapezium has disappeared in the horse, but the three other bones remain, and the middle one is the largest, as in the rhinoceros. The extinct Palæotherium offers a connecting link in the transition to the apparently monodactyle foot. The trapezoïdes (*z*) and unciforme (*u*) are however still more reduced in size, in the horse, corresponding with the reduction of the toes, which they support, to mere styliform remnants of their metacarpal bones; and the os magnum and its metacarpal bone are proportionally increased in bulk.

Thus not only are the first and fifth digits wanting in the horse, but the second and fourth are rudimental, and only the third is retained complete, and it constitutes almost the entire foot. The cannon-bone of the horse is not therefore composed, like that of the ox, of two metacarpals confluent, but is essentially as well as actually a single bone; and accordingly it supports a single toe of three phalanges, which, in the special language of the Hippotomist, are the 'great pastern-bone' (1), the 'small pastern-bone' (2), and the 'coffin-bone' (3); the little sesamoid behind the last joint being called the 'navicular' or 'nut' bone*.

* The common term 'cloven-hoof,' applied to the foot of the Ruminants, indicates the idea that it was the solidungulous foot split up; and the converse in respect of the horse's foot has been taught by high and justly esteemed authorities. Sir Charles Bell, in his 'Bridgewater Treatise,' 8vo, 1833, states, p. 82, "In the horse, the cannon-bone may be shown to consist of two metacarpal bones." But he does not give the demonstration. He refers (p. 85) to a comparison which led him to view the phalanges as still more compounded. "In looking

A perfect and beautiful parallelism reigns in the order in which the toes successively disappear in the hind-foot with that in the fore-foot. The 'hallux' or inner toe, answering to the great-toe in man, is the first to fade away: *e. g.* in the dog (Pl. I. fig. 5), where its rudiment may be found (*i* 1, 69) with a slender entocuneiform (*c i*): in the hippopotamus both the digit and its tarsal bone are wanting. The outer or fifth toe, answering to the little toe in man, is reduced to a rudiment in the alactaga, and totally disappears in the tapir and rhinoceros, where fig. 17, Pl. I. shows the middle toe in its normal relation with the ectocuneiform, the second toe with the mesocuneiform—now the internal bone, and the fourth toe with the reduced cuboides. Fig. 18 shows that the toe which next disappears, *e. g.* in the hind-foot of the Ruminant, is the second, as in the fore-foot; the third and fourth being retained to support the 'cloven-hoof'; the one articulating with the ectocuneiform (*c e*), the other with the cuboid (*b*), here confluent with the scaphoid. The rudiments of the second (*ii*) and fifth (*v*) digits appear externally as the 'spurious hoofs,' which dangle or project behind the normal one. These, however, are not without their use: when the elk or bison treads in swampy ground, the hoofs expand, the false hoofs are pushed out, and the resisting surface is increased as the

to this sketch and comparing it with that of the hand on page 79, we see that in the horse's leg the five bones of the first digital phalanx are consolidated into the large pastern-bone; those of the second phalanx into the lesser pastern or coronet; and those of the last phalanx into the coffin-bone." The learned Professor of Comparative Anatomy in University College, London, describing the bones of the horse's foot, also says,: "We observe that the phalanges, three in number in each toe, of the anterior and posterior extremities, are composed each of two bones anchylosed together, so that only one toe appears to touch the ground, which is covered with a large undivided hoof, from which they are called '*Solidungula*'." And again: "The anchylosis seen in the cannon-bone of the Ruminantia has here proceeded downwards through the whole extent of the feet."—*Dr. Grant's Lectures*, '*Lancet*,' No. 550, March 1834, p. 907.

foot sinks; but when it is lifted up the small hoofs collapse to the sides of the large ones, which contract, and by this diminution of the size of the foot the act of withdrawal is facilitated*.

In the Ruminants confined to arid deserts we should hardly expect to meet with the mechanism which seems expressly adapted to the marsh and the swamp; and in fact every trace of the second and fourth digits has disappeared from the feet of the camel and dromedary. The comparison of the bones of the extremities is replete with these beautiful evidences of design; but our present purpose is to gather the indications of that which has been sometimes, but wrongly, regarded as the antithetical principle, viz. the unity of plan which lies at the bottom of all the adaptive modifications.

In the hind-foot of the horse you will perceive that the homologue of our small external cuneiform bone (*ce*, fig. 6, Pl. I.) has attained an excessive size in fig. 19, *ce*, and that the toe (*iii*) which that bone supports throughout the Mammalian series is correspondingly developed; whilst the mesocuneiform (*m*) and the cuboid (*b*) are in an equal degree reduced, and, like their carpal homotypes the trapezoid and unciform, they support only rudiments of the second and fourth metatarsals in the form of the accessory splint-bones (*ii* and *iv*).

To sum up, then, the modifications of the digits: they never exceed five in number on each foot in any existing vertebrate animal above the rank of Fishes; and in the class *Mammalia*, the *Cetacea* excepted, the number of phalanges is limited to two in the first digit and to three in each of the other digits, in both fore- and hind-feet. In the cuts and in each figure of Pl. I. they are numbered from the innermost, I, II, III, IV, V, in the fore-foot, and *i*, *ii*, *iii*, *iv*, *v*, in the hind-foot: these are their symbols, and are

* Sir Charles Bell has well shown the advantage of the cloven hoof over the undivided hoof in this respect, *op. cit.* p. 89.

applied arbitrarily to their objects; thus the digit (*ii*) in the rhinoceros is the innermost or first of its series, and the digit (*iv*) is the third; but the notation signifies in this and all the figures that the digits *ii*, *iii*, or *iv*, are those answering to the second, third and fourth in the fully-developed foot.

The first or innermost digit, as a general rule, is the first to disappear; in the hind-foot of the orang (fig. 14) commonly, and in that of the wombat (fig. 16) constantly, its short metatarsal supports but one phalanx; in the dog (fig. 4), the inner digit is usually wanting in the hind-foot, and is always very diminutive in the fore-foot. The first digit of the hand is reduced to a short metacarpal in the spider-monkeys (*Ateles*).

The outer digit v and *v* is the next to disappear. In the tapir it is wanting in the hind-foot; and in the rhinoceros (fig. 17) in both hind- and fore-feet.

In the bisulcate quadrupeds the development of the second digit (*ii*) is arrested in addition to the outermost one (v), and the functions of support and progression are committed to the equally and symmetrically developed digits *iii* and *iv*: rudiments of the second and fifth digits are retained in most Ruminantia (as at *ii* and *v*, fig. 18); but in the camel-tribe they have entirely disappeared, together with the first digit, I and *i*.

In the horse (fig. 19) the fourth digit is the additional subject of arrested development, and the median one in both fore- and hind-feet, III and *iii*, is the last and sole digit which retains its full and functional perfection, thus manifesting its character as the most constant and essential of the terminal ramifications of the primitive ray which we saw in the lepidosiren.

Whilst the number of toes is thus seen to fall short, progressively, of five, the typical character of that number is still indicated by the power of determining the particular toe or toes of the five in man, which are retained in the tetradactyle, tridactyle, didactyle and monodactyle feet re-

spectively of the lower mammals. But although the number 'five' thus governs the development of digits, properly so called, in all existing air-breathing Vertebrata, the tendency to multiplication of terminal rays in the diverging appendages modified for locomotion may be seen to manifest itself in the sexual 'spurs' of the Gallinaceous birds and Monotremes; in the hereditary supernumerary toes in certain varieties of the common fowl, and even in some individuals of the human race. But the single spur of the tetradactyle cock is not more a homologue of a normal digit in a pentadactyle reptile or mammal, than is the spur of the *Platypus*, or either of the spurs in the *Pavo bicalcaratus**.

So long as the digits are developed as simple rays they are not subordinated to the typical number, but usually much exceed it, as we find in most fishes. In the skate (*Raia*), indeed, the pectoral members far surpass in bulk and seeming complexity their homologues in man: but their development is of a lower kind: it consists of a vegetative repetition,—division, bifurcation and segmentation—of mere rays, of a multiplication of essentially similar parts, without power of reciprocal action and reaction on one another; all being bound up in one common fold of integument for one simple kind of flapping motion—the only one required for an animal so low in the scale, but perfectly provided for by the form of fin in question. At first sight the pectoral fin of the skate with its hundred digits seems a more complex deviation from the primordial single ray, as shown in the lepidosiren (Pl. I. fig. 7), than the pentadactyle upper extremity (fig. 6, 53—57) of man; but this is far from being the case: true complexity is not shown in the number, but in the variety and coordination of parts.

The high characteristics of the human arm and hand are manifested by the subordination of each part to a harmonious combination of function with another, by the de-

* These horny appendages of the metatarsus appear rather to be homotypes of the strong quills attached to the metacarpus in birds.

parture of every element of the appendage from the form of the simple ray, and each by a special modification of its own; so that every single bone is distinguishable from another: each digit has its own peculiar character and name, and the 'thumb,' which is the least constant and important of the five divisions of the appendage in the rest of the class, becomes in man the most important element of the terminal segment, and that which makes it a 'hand' properly so called.

In the pelvic, as in the scapular extremity, the same digit (*i*), which is the first to be rejected in the mammalian series, becomes, as it were, 'the chief stone of the corner,' and is termed 'par excellence,' the 'great-toe:' and this is more peculiarly characteristic of the genus *Homo* than even its homotype the thumb; for the monkey has a kind of *pollex* on the hand, but no brute mammal presents that development of the *hallux*, on which the erect posture and gait of man mainly depend.

We perceive, however, that although the first toe (Pl. I. fig. 6, *i*) is the longest as well as the largest, it retains its characteristic inferior number of phalanges; its bulk depending, like the larger toe in the didactyle ostrich (fig. 11, *iii*), on the superior size instead of an increased number of bones; whilst the fifth or little toe (*v*) still retains with diminished proportions its full complement of phalanges. The teleologist will discern that the requisite strength of the toe, which is the chief fulcrum when the whole body is raised by the power acting on the heel, as in stepping forward, has been regarded in the diminished number of its joints; but the same final cause would not appear to have governed the different number of joints of the equally-sized first and fifth of the five toes inclosed in the massive hoof of the elephant or the webbed hind-paddle of the seal: and whether the hallux be the shortest of the five or the longest, it has always the same number of phalanges whenever it is present, provided it supports a nail, a hoof or a claw, in the mammalian series.

The satisfaction felt by the rightly constituted mind must ever be great in recognising the fitness of parts for their appropriate functions; but when this fitness is gained, as in the great-toe of the foot of man and the ostrich, by a structure which at the same time betokens harmonious concord with a common type, the prescient operation of the One Cause of all organization becomes strikingly manifested to our limited intelligence.

It is interesting to perceive both in the human hand and foot that the digits that have been most modified either by excess or defect of development are precisely those that are the least constant in the mammalian series—the two, for example, that form the extremes of the series; whilst the three intermediate digits are more conformably and equably developed. In the hand, the 'digitus medius'—the most constant of all in the vertebrate series, and most entitled to be viewed as the persistent representative of the terminal segments of the primitive elementary ray,—still shows a slight superiority of size; though few would be led thereby to suspect that the bones forming the three joints of this finger answer to those called 'great pastern-bone,' 'little pastern-bone,' and 'coffin-bone' in the horse, and that the nail of this finger represents the hoof in the horse.

In the human foot the three more constant toes, *ii*, *iii*, *iv*, maintain more equality of size than their homotypes in the hand: the middle toe here also is the representative of the chief part of the hind-foot of the horse: but the fourth toe answers to that which, by excess of growth, becomes the chief member of the long and strong hind-foot of the kangaroo. These and the like relations to the Vertebrate archetype, which, together with the principle of the fitness of things, govern the forms and proportions of parts of the human frame, cannot but be both interesting and useful to the artist, as being calculated to call his attention to differential characters, which, though constant, may be so slight as to escape attention until their true significance is made known.

The few examples of unmutilated feet from the works of the ancient Greek sculptors show, indeed, how truly their just observation of nature supplied the insight into the archetypal law, and guided them to an exact and beautiful indication of the affinities of the three middle toes as contrasted with the first and fifth, the distinctive characters of the last being as truly given as those of the great-toe *.

If we pause to take a retrospect of the ground over which we have been travelling, and consider the numerous and beautiful evidences of unity of plan which the structures of the locomotive members have disclosed,—evidences so little to be expected, *à priori*, seeing the different shapes and sizes of instruments adapted to such diversity of functions;—when also we find that besides the general conformity of structure in the limbs of different species, a more special parallelism could be traced between the fore- and hind-limbs of the same species, no matter to what diversity of office they might be severally adapted—a parallelism or 'serial homology' demonstrable even to each little carpal and tarsal bone, from man down to the monodactyle horse,—the thinking mind cannot but be forcibly struck by such facts, and be impelled with the desire to penetrate further, and ascend if possible to the higher law or generalization from which those harmonies flow.

I think it will be obvious that the principle of final adaptation fails to satisfy all the conditions of the problem. That every segment and almost every bone which is present in the human hand and arm should exist in the fin of

* I have elsewhere cited examples from some great painters in which these characters have been overlooked, and the toes drawn "small by degrees and beautifully less" from the second to the fifth: the natural proportions given to the feet of the dead Saviour by the truthful and severe Francia, and by Sebastian del Piombo to those of the figures in the "Raising of Lazarus," contrast favourably with the conventional feet in some of the paintings by Correggio and Guido in our National Gallery.

the whale, solely because it is assumed that they were required in such number and collocation for the support and movements of that undivided and inflexible paddle, squares as little with our idea of the simplest mode of effecting the purpose, as the reason which might be assigned for the great number of bones in the cranium of the chick, viz. to allow of the safe compression of the brain-case during the act of exclusion, squares with the requirements of that act. Such a final purpose is indeed readily perceived and admitted in regard to the multiplied points of ossification of the skull of the human fœtus, and their relation to safe parturition. But when we find that the same ossific centres are established, and in similar order, in the skull of the embryo kangaroo, which is born when an inch in length, and in that of the callow bird that breaks the brittle egg, we feel the truth of Bacon's comparison of 'final causes' to the Vestal Virgins, and perceive that they would be barren and unproductive of the fruits we are labouring to attain, and would yield us no clue to the comprehension of that law of conformity of which we are in quest. And so, again, with regard to the structural correspondences manifested in the locomotive members; if the principle of special adaptation fails to explain them, and we reject the idea that these correspondences are manifestations of some archetypal exemplar on which it has pleased the Creator to frame certain of his living creatures, there remains only the alternative that the organic atoms have concurred fortuitously to produce such harmony*.

But from this Epicurean slough of despond every healthy mind naturally recoils: and reverting therefore to the hypothesis of the dependence of special and serial homologies upon some wider principle of conformity, we have next to inquire, what is the archetype or essential nature of the limbs?

* *Ἀπὸ τῶν ἀτόμων σωμάτων ἀπρονόητον καὶ τυχαίαν ἐχόντων τὴν κίνησιν.—Epicurus.*

Cuvier seems to have regarded the science of Comparative Anatomy to be not sufficiently advanced to enter upon this analysis with any prospect of success.

Oken's idea of the essential nature of the arms and legs is, that they are no other than 'liberated ribs'; "Freye Bewegungsorgane können nichts anderes als frey gewordene Rippen seyn*."

Carus, in his ingenious endeavours to gain a view of the primary homologies of the locomotive members, sees in their several joints repetitions of vertebral bodies (*tertiar-wirbel*)—vertebræ of the third degree†—a result of an ultimate analysis of a skeleton pushed to the extent of the term 'vertebra' being made to signify little more than what an ordinary anatomist would call a 'bone.' But these transcendental analyses sublime all differences, and definite knowledge of a part evaporates in an unwarrantable extension of the meaning of terms.

I believe, however, that I have satisfactorily demonstrated that a vertebra is a natural group of bones, that it may be recognised as a primary division or segment of the endoskeleton, and that the parts of that group are definable and recognizable under all their teleological modifications, their essential relations and characters appearing through every adaptive mask‡.

Subjoined is a view of such a natural segment as it exists in the thorax of a bird. c is the 'centrum,' which was originally a separate element: *n*, one of the walls of the canal for the 'spinal marrow' (myelon or trunk-portion of the neural axis); it was originally distinct from the centrum and from its fellow of the opposite side; it is the 'neurapophysis': *pl* indicates another pair of elements—the 'pleurapophyses,' which here maintain their primitive

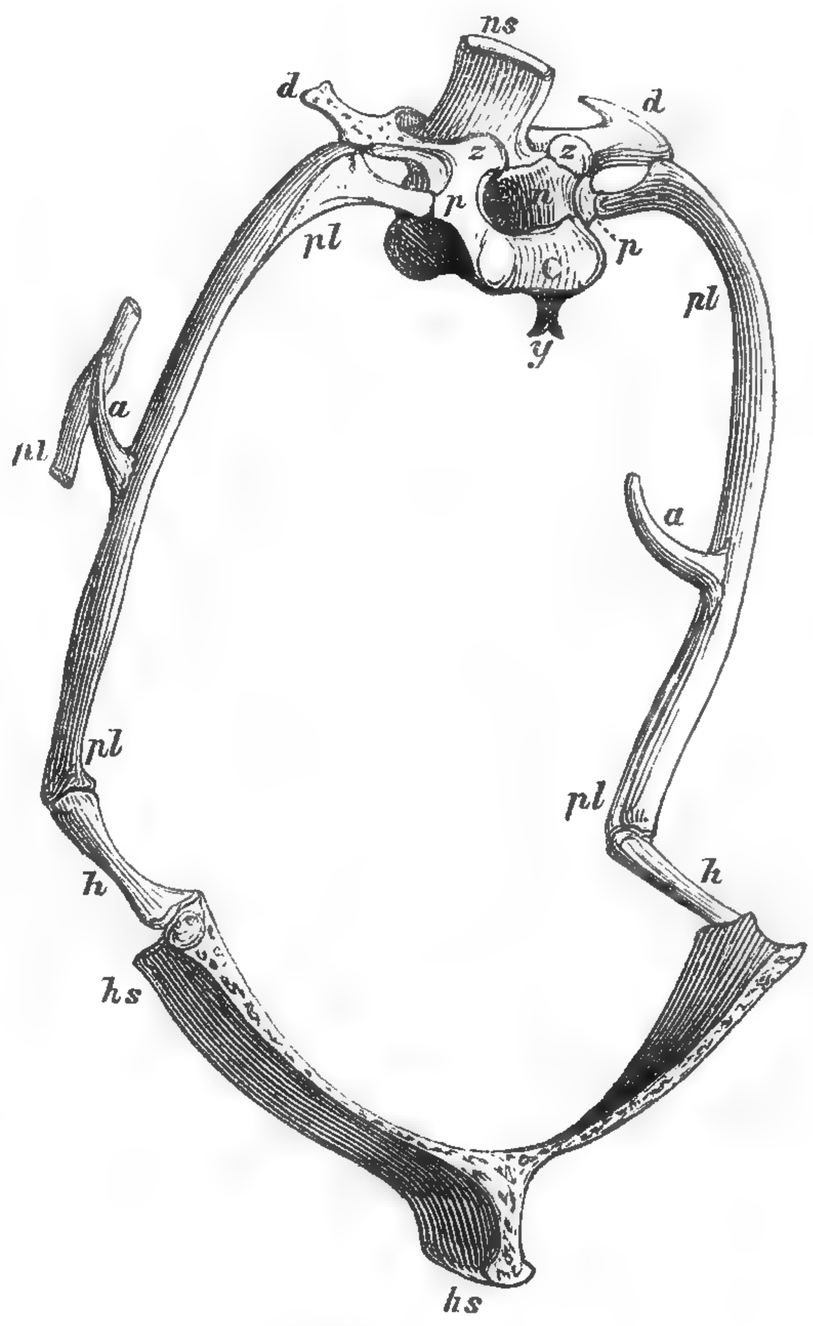
* Lehrbuch der Natur-Philosophie, p. 330, 8vo, 1843.

† Urtheilen des Knochen und Schalengerüstes, fol. 1828.

‡ 'On the Archetype of the Vertebrate Skeleton,' 8vo, 1848, pp. 80—102.

distinctness, and grow long in order to aid in encompassing the dilated canal or cavity for the great vascular centres: so modified, these elements are called 'ribs' or vertebral ribs. The elements more constantly related to the

Fig. 7.



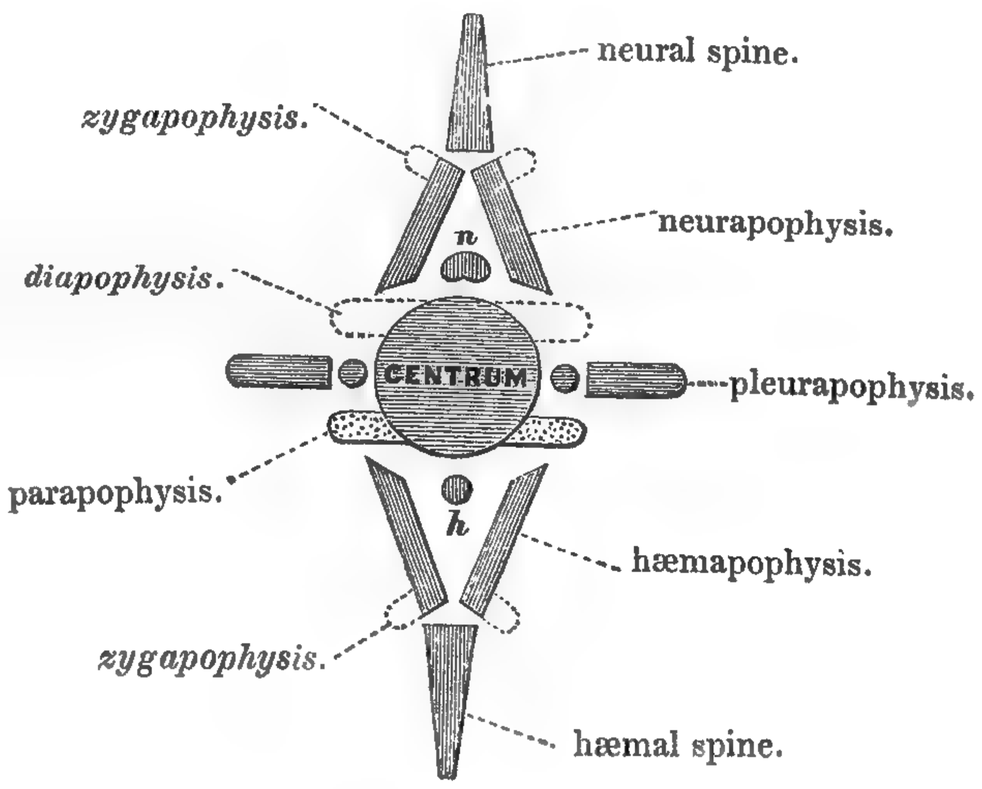
Natural skeleton-segment, 'osteocomma' or 'vertebra.' Thorax of Bird.

protection of the vascular or hæmal axis are those marked *h*, the 'hæmapophyses,' here displaced from the centrum by the development of the heart and lungs and other organs of the embryonic vascular layer: they then get the special name of 'sternal ribs,' or that of 'costal cartilages' when their ossification is arrested. The hæmal arch is here completed by an unusually expanded 'hæmal spine,' *hs*, which coalesces with those of contiguous segments, and they are then collectively denominated the 'sternum.' The

neural arch is completed by an answerable piece above, *n s*, which here retains its normal size and form as a 'neural spine.' But, where the neural canal is expanded for great developments of the nervous centres, the brain, *e. g.*, analogous to the development of the vascular centres in the 'thorax,' the neural canal is correspondingly expanded and forms a 'cranium': other elements besides the 'neurapophyses' enter into the formation of its walls, and the 'neural spine' is expanded horizontally, often retains its individuality, and, like the 'sternum' in the thorax of the bird, receives a special name, *e. g.* 'parietal' or 'frontal.' Two other distinct elements, *a*, *a*, in fig. 7, are attached at one end to the hæmal arch, and project backwards, overlapping, in the bird, the succeeding arch. Less constant, secondary or derivative processes more or less complicate the typical segment, but are not essential to it: of these are shown in fig. 7, *zz* the 'zygapophyses,' *pp* the 'parapophyses,' *dd* the 'diapophyses,' and *y*, the 'hypapophysis.'

As the expanded nervous centres contract to a column or trunk of moderate and pretty uniform diameter, so also do the vascular centres; and where the vascular axis is reduced to the dimensions of the nervous axis above, the

Fig. 8.



Ideal typical vertebra.

vertebra resumes a more symmetrical character, by the corresponding reduction of the hæmal arch: in the crocodile, *e. g.* this is formed by the hæmapophyses which ascend to contact with the centrum; the pleurapophyses being shortened, projecting outwards, and anchylosed as processes: but such a vertebra, when analysed as it is developed, resolves itself very nearly into the ideal type given in the diagram fig. 8.

n is the neural axis or myelon, and *h* the hæmal axis or aorta, protected by their respective arches. The Roman type is used for the 'autogenous elements,' or those usually developed from distinct centres of ossification; and the italics denote the parts more properly called 'processes' which shoot out from the preceding elements.

On comparing this form of the segment with the foregoing one, it will be seen that they differ by altered proportions with changed positions of certain elements; but it is important to our present inquiry to notice that in figure 7 there is an additional bone marked *a* which projects as an appendage from each side of the hæmal arch.

As we find such appendages in the thoracic segments of the crocodile (Pl. I. fig. 3, *a*, *a*), and in the corresponding abdominal segments of the skeleton of most bony fishes (*ib.* fig. 2, *a*, *a*), where they are usually longer, and extend through the flesh to the skin, we may regard them also as parts of the primitive segment or vertebra, though less constant than the arches that support them.

The attempt to decipher the essential nature of limbs will lead us in the first place to their comparison with one or other of the elements of the typical segment. And, having arrived at the demonstration of such segment, and proved that every modification of the axis of the skeleton has its seat in one or other of the segmental or 'vertebral' elements, we may enter upon this track of inquiry with hopeful confidence in the results.

I have already observed that Oken selected the rib as

the seat of those developments from which the varied forms of the limbs of animals result: the truth of this idea will be tested by tracing the progressive simplification of the limb in the Vertebrate series.

We already find it in the Mammalian series reduced almost to one long jointed ray in the horse (fig. 4), two other terminal forks being feebly indicated by the little splint-bones. In the lower Reptilia we find the limbs progressively diminish in relative bulk to the body and to their sustaining arch. In the amphiuma (Pl. I. fig. 8) each limb is a jointed appendage, consisting first of a single segment (53), then of a bifid segment (54 & 55), lastly of a bifid (57) or a trifid segment (*A. tridactylum*); in these segments we have the homologues respectively of the humerus or femur, of the two bones of the fore-arm or leg, and of the three middle and most constant toes. In the proteus (fig. 10) the terminal forks are diminished to two on the hind-limb, and in the *Amphiuma didactylum* to two digits on both fore- and hind-limbs. In the apteryx (fig. 9) the second segment of the stunted fore-limb is bifid, but the last segment is simple or monodactyle. One other step in the series, and, in the lepidosiren, we find the limb reduced to an unbranched ray, modified only by a vegetatively multiplied succession of simple segments (Pl. I. figs. 7 & 9).

But in none of these instances do the limbs diverge, like the free or false ribs in the parachute of the little flying dragon, from the vertebral centrums or neural arches.

Under whatever grade of structure the limbs exist, they are supported by inverted arches, the anterior being the 'scapular arch,' the posterior the 'pelvic arch': and these arches remain when every trace of limb has disappeared; as for example, the scapular arch in the *Anguis* and *Muræna*, and a rudiment of the pelvic arch in the Cetacea.

The question, therefore, which we have now to determine

is, what is the nature or general homology of these arches? and first of the scapular arch?

Of the special homology of its parts, to the extent that we have traced them, there exists I believe no difference of opinion amongst anatomists.

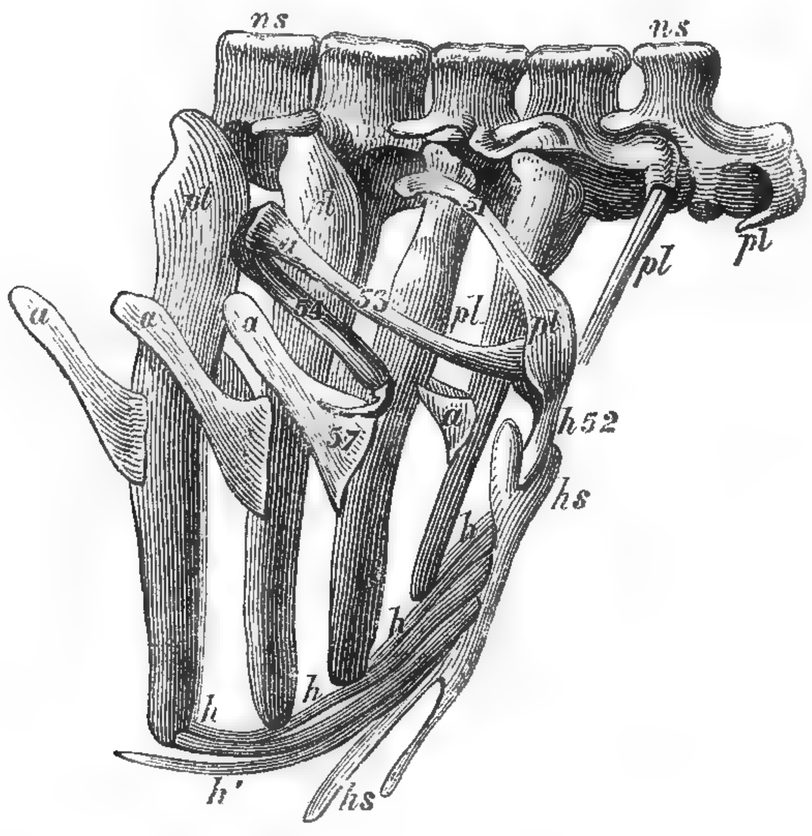
The scapula is usually as broad and flat in mammals as the first rib of the whale is; it becomes narrow and vertical in the ornithorhynchus; continues long and slender in birds and saurians; is a columnar rib-like bone in the Chelonia, where it is as straight as the first rib in the ox; and it retains the same form in the amphiuma (Pl. I. fig. 8, 51) and lepidosiren (*ib.* fig. 7, 51).

The scapula is the upper element or pier of an inverted arch, completed, with a few exceptions, by a second elongated bone, converging towards its fellow on the opposite side, and joining it either directly or through the medium of a single interposed key-bone, called 'sternum,' which bone answers below to the key-bone or 'spine' of the neural arch above. The special name of the second bone is the 'coracoid.' The crocodile (Pl. I. fig. 3) affords a good example of the proper scapular arch so composed, *i. e.* consisting of a pair of scapulæ (51), a pair of coracoids (52), and the sternum or episternum (52′).

In all reptiles and in all birds the arch is thus completed: in fishes the coracoids meet without the interposition of a sternum (Pl. I. figs. 2 & 7, 52). In most oviparous vertebrates the arch is complicated by a second inferior element, parallel or nearly so with the coracoid; behind it in fishes (fig. 2, 58), before it in reptiles, birds (fig. 4, 58) and monotremes: this accessory bone is the 'clavicle': when it unites below with its fellow, as in birds, it is called the 'merry-thought' (*os furcatorium*); but it is wholly wanting in some species, as in certain ground parrots and the apteryx (fig. 9). The clavicle is wanting altogether in entire groups of Mammalia, *e. g.* in the Cetacea, and in all the Hoofed orders. But the coracoid is always

present, although its complete development, which is the rule in the lower classes of Vertebrata, becomes the exception in Mammalia, where it reaches the sternum only in the ovoviviparous ornithorhynchus and echidna. In the rest of the class the coracoid projects as a longer or shorter process from the scapula, but differs from the other 'processes' of that bone in having a separate centre of ossification; it is, in short, an autogenous element, whilst the 'spine' and 'acromion' are merely exogenous growths.

Fig. 9.



Part of the thorax with the scapular arch and appendage. *Apteryx australis.*

In many Mammalia the clavicle appears to take the place of the fully-developed coracoid of the Ovipara, and completes the scapular arch by extending from the acromion to the sternum, as *e.g.* in our own skeleton (Frontispiece and Pl. I. fig. 6, 58*). But it will be readily understood by what has been stated with regard to the relative constancy, both as to connexion and existence, of the coracoid, that this is the true inferior element of the scapular arch, and

* A front view of the human scapular arch is given at p. 46 of Sir C. Bell's 'Bridgewater Treatise.'

that its place is, so to speak, usurped by the clavicle in man, just as the chain of suborbital bones in the skull of the fish takes the place of the true zygomatic arch of higher Vertebrates*.

Leaving, however, for the present the discussion of the general homology of the clavicle, and returning to that of the scapular arch, as it exists in its integrity and simplicity, in the apteryx or crocodile, the question before us is, with what part of the typical segment of the vertebral skeleton can it best be compared? The answer is at once suggested by the hæmal arch, as it exists in the thoracic region of any air-breathing vertebrate, in which the parallel parts are obviously presented in similar connexion with each other. The scapula (Pl. I. fig. 7, *pl*) answers to the pleurapophysis or vertebral rib (p. 42, fig. 7, *pl*), the coracoid (*h*) to the hæmapophysis or sternal rib (*h*), and the scapular arch is completed in most vertebrates by a bone of the sternum or hæmal spine (Pl. I. fig. 3, 52′). In harmony with this determination is the interesting correspondence in the range of its diversities of form and proportion which the scapula presents with that which may be traced in the thoracic pleurapophyses or 'vertebral ribs.' I have already cited the whale, *e. g.* as manifesting such a 'rib' with proportions as broad and flat as any mammalian scapula; and numerous instances will occur to the anatomist of 'ribs' that are as long, narrow, compressed and gently curved as is the scapula in the bird; or that are straight and columnar like the scapula in the tortoise.

Any difficulty of appreciating or hesitation in accepting such general homological views by the anthropotomist arises, he may be assured, from his habitual and exclusive contemplation of the vertebral element in question under one only of its morphological phases, and that usually an extreme and an exceptional one. Even the steps in the progressive degradation of the true scapular arch which we

* On the Archetype of the Vertebrate Skeleton, p. 62.

witness in the mammalian class are closely paralleled by the ordinary costal arches: thus the twelfth vertebral rib in man, with its sternal rib or cartilage curtailed and appended to its free extremity, as a process, repeats the condition of the scapula with its shortened coracoid appended and anchylosed to it, as a process, in man also, and in most mammals.

The posterior costal arch in the bird's thorax, to the sternal rib (hæmapophysis) of which may be attached the same element of a contiguous arch, unconnected with its proper vertebral rib, as seen in the apteryx (fig. 9, *h*, *h'*), parallels that condition of the scapular arch where it is complicated by an appended clavicle,—the hæmapophysis of a second inverted arch.

The scapula, however, differs, in most of the higher Vertebrata, from the thoracic ribs in being more or less turned from the perpendicular to the horizontal direction: this is particularly the case in birds, where it lies almost at right angles across those ribs, as in fig. 4, Pl. I. Its progressive assumption, however, of the vertical position, or one more or less parallel with that of the ordinary ribs, as the species descend in the scale, would have much weight, in forming a judgment as to the essential nature of the scapula, with the physiologist who appreciated the law that the Archetype is progressively departed from as the organization is more and more modified in adaptation to higher and more varied powers and actions. But what is still more significative of the nature of the scapula is the discovery that its vertical position in reptiles and fishes is a retention of that position which the bone manifests on its first appearance in all Vertebrata. The rotation of the scapula from its primitive verticality to whatever approach to the horizontal line, or axis of the vertebral bodies, the exigencies of the full-grown animal may require, its primitive appearance close to the occiput, and its longer retention of a place anterior to the first thoracic

rib, are developmental phænomena which cease to be mere empirical facts*, but receive their explanation and become intelligible by the recognition of the general homology of the scapula which I am now attempting to illustrate.

Sufficient, I trust, has been adduced to show that, of all the elements of the typical vertebra or primary segment, the scapula can be compared only with the 'pleurapophysis,' and the coracoid only with the 'hæmapophysis.' But it may be objected, that the ordinary costal or hæmal arch has been detached from its centrum for the purpose of this comparison. True! And the scapular arch in mammals, birds and reptiles is a hæmal arch so dislocated,—a statement which I do not hesitate to make under a pledge to demonstrate the proper centrum and the rest of the segment or vertebra to which it belongs.

In the first place I may remark, that the dislocation of parts of admitted costal or hæmal arches is no new thing. Why does the human anatomist refer the fourth costal arch to the fourth dorsal vertebra and not to the fifth, to the centrum and neurapophyses of which it is equally connected? The head of the rib is applied half to one centrum half to the other: the upper border of the neck of the rib, viewed in the upright skeleton, articulates with the upper neural arch, the tubercle of the rib with the diapophysis of the lower neural arch: the human anatomist, in restoring this displaced hæmal arch to its proper segment, has availed himself of the same kind of inquiry and comparison† which has been instituted in order to detect the segment from which the scapular arch has strayed. The same kind of comparison was equally requisite in order to determine

* See Rathké, 'Ueber die Entwickelung der Schildkröten,' 4to, 1848, pp. 182, 183. The different position of the scapula in fig. 9, 51, from that in the typical Bird's skeleton (Pl. I. fig. 4, 53), is due to a retention of an embryonic phase in the apteryx.

† See 'On the Archetype of the Vertebrate Skeleton,' pp. 118, 119.

the true segments to which the displaced neural arches in the sacrum of the bird belonged*.

But here let us examine how far down the vertebrate scale the scapular arch continues to manifest itself as a hæmal arch displaced: and let us ascertain whether Nature affords us any instance of such a retention of the ideal type as would be exemplified by the connection of that hæmal arch with its proper centrum and neural arch? The object we are in quest of is soon attained.

The desired instance is mostly clearly and satisfactorily afforded by the eel-like fish to which I have already referred as affording the most simple type of locomotive extremity, I mean the lepidosiren. We see that the upper element of the arch is now articulated to the neural arch of the occipital vertebra: and if we remove this segment of the skull and take a full view of it, as in fig. 7, Pl. I., we have a vertebra which closely conforms to the typical one illustrated by the thoracic segment of the bird, p. 42, fig. 7. In both figures, *c* is the centrum, *n* the neurapophyses, *s* the neural spine, *pl* the pleurapophyses, and *h* the hæmapophyses: the hæmal spine alone is wanting to complete the parallel: and we know that it is not more essential to the composition of the hæmal arch, than the neural spine is to the completion of the neural arch.

There can be no doubt that the bone which represents the rib or hæmapophysis in the occipital segment of the amphibious fish (Pl. I. fig. 7) is the bone which receives the special name of 'scapula' in higher animals. We have traced it under all its modifications down to the low batrachian reptile (Pl. I. fig. 8), in which its special homology was clearly recognised by Cuvier; and between the straight columnar upper element (51) of the inverted arch which supports the simple pectoral limb of the amphiuma, and the upper element (51) of the inverted arch which supports the still more simple limb in the lepidosiren, the resem-

* 'On the Archetype of the Vertebrate Skeleton,' pp. 118, 159.

blance is much closer than that between the scapula of man and the scapula of the mole, or between this and the scapula of the ornithorhynchus.

Since also comparative anatomists have arrived at one conclusion in respect to the homology of the stunted coracoid in man with the coracoid element that stretches from scapula to sternum in the ornithorhynchus and all air-breathing Ovipara, it would be captious to deny the same relationship between the coracoid of the amphiuma (*h* 52) and that of the lepidosiren (*h* 52). The sole fact lending colour to such negation is the slight difference in the place of attachment of the diverging appendage, which is wholly in the coracoid in the lepidosiren, instead of partially, as in the amphiuma,—a difference which, with that in the upper connections of the scapula, is characteristic of their respective classes.

The main fact, then, is established, viz. that the inverted arch (51, 52, fig. 7, Pl. I.) which supports the pectoral ray in the lepidosiren is the scapular arch, and Nature here shows us its attachment to the occiput (*c* 1, *n* 2, *s* 3) in the relation of the hæmal arch of the occipital vertebra.

Nor is the lepidosiren an exceptional instance of this connection and relation. It forms but one of a vast class of Vertebrata—by far the most numerous and widely-dispersed class—which manifest the same attachment of the scapular arch. The pectoral fin (Pl. I. fig. 2, 54–57, *a*) which consists, in most fishes, of a multiplication of jointed rays like that of the lepidosiren, is supported by an inverted bony arch, attached to the neural arch of the occiput, and completing that segment of the skeleton by forming its hæmal arch*. Whatever be the size, form or function of the pectoral limb, its supporting arch maintains this position and connection in all osseous and some cartilaginous (Chimæroids, Sturionidæ) fishes: and here, also, we find

* 'Archetype of the Vertebrate Skeleton,' p. 107.

the arch in the *Muræna* and *Gymnothorax*, in which every trace of its appendage, the pectoral fin, has disappeared.

How then is this connection of the scapular arch to be interpreted? If we were prepossessed by the habitual contemplation of its detached state in man and the higher Vertebrata, we might deem such occipital connection an anomaly, an 'instantia devians,' and so in fact it has hitherto been viewed by those anatomists who have entered into the study of the higher generalizations of their science. Geoffroy St. Hilaire, one of the boldest speculators in the mine of transcendental ideas, calls it in his 'Anatomie Philosophique' (p. 481) 'une amalgame inattendue:' and in one of his Memoirs speaks of it as "Disposition véritablement très singulière, et que le manque absolu de cou, et une combinaison des pièces du sternum avec celles de la tête pouvoient seuls rendre possible *."

We no longer, however, believe that the vertebræ of the neck are absolutely wanting in fishes; but recognize them with their pleurapophyses more normally or typically developed than in the corresponding region of the crocodile. Homotypes of the thoracic sternal bones are doubtless present in the head of fishes, as in that of other Vertebrates, where they are exemplified by the basihyal (see 41, figs. 2 to 6, Pl. I.); but it is not requisite to conclude that the median bones (41, 42, 43, fig. 2) of the hyoid arch, or the analogous ossicles of the transitory splanchnic branchial arches, in fishes, are the homologues of 59 and 60 in figs. 3 to 6, Pl. I., in order to arrive at the comprehension of the connection of the scapular arch with the occipital vertebra in the lepidosiren and the majority of its class.

Viewing that vertebra, like the other natural segments of the skeleton, to be conformable to the type as illustrated by fig. 7, p. 42, it would be incomplete without the hæmal arch formed by the scapula and coracoid. And further, there

* Annales du Muséum, tom. ix. p. 361.

is no other arch which could so complete the occipital vertebra. There are three neural arches in advance of the occipital one, in fig. 2, viz. the parietal (5, 6, 7, 8), the frontal (9, 9′, 10, 11, 12), and the nasal (13, 14, 15); and there are three hæmal arches, viz. the maxillary (20, 21, 22), the mandibular (28, 29, 32), and the hyoid (38, 39, 40, 41). With the exception of the hyoid arch, which is slightly depressed, each of these hæmal arches is directly connected with its respective neural arch, just as the scapular arch is connected with the occipital: there is no other arch to supply the place of the hæmal one of the occipital segment, if the scapular arch be removed.

Are we then to view the instances of its detachment from its piscine connections as exemplifying the normal or typical conditions of such arch? Surely not; as well might we consider the displaced hæmal arches of the human thorax to manifest their typical positions and connections, and regard their direct and exclusive connections with their proper centrums in reptiles and fishes as the exception and the anomaly. But that which has happened to the crocodile in the restoration of the ribs, homologous to the second and tenth inclusive of man, each from the interspaces of two vertebræ to the body and neural arch of one vertebra, *i. e.* to the connections which the first, eleventh and twelfth ribs retain in the Human skeleton, has likewise taken place in fishes in regard to the modified rib forming the scapula. So true is the Baconian aphorism regarding the power of interpretation consequent upon the knowledge of the archetype or 'via Naturæ!' "Inter prærogativas instantiarum ponemus loco octavo *instantias deviantes*; errores scilicet naturæ, et vaga ac monstra: ubi natura declinat et deflectit a cursu ordinario. Differunt enim errores naturæ ab instantiis monodicis in hoc, quod monodicæ sint miracula specierum, at errores sint miracula individuorum. Similis autem fere sunt usus; quia rectificant intellectum adversus consueta, et revelant formas

communes. Neque enim in his etiam desistendum ab inquisitione, donec inveniatur causa hujusmodi declinationis. Veruntamen causa illa non exsurgit ad formam aliquam proprie, sed tantum ad latentem processum ad formam. Qui enim vias naturæ noverit, is deviationes etiam facilius observabit. At rursus, qui deviationes noverit is accuratius vias describet*."

Most of the mistakes in the attempts to ascertain the typical or essential nature of parts of the skeleton, and almost all the impediments and opposition to the prosecution of this main end of anatomical science, have arisen from its study being confined to that by-path in which it is usually commenced, viz. where the course of development has reached the highest form of animal life, in which modification of each part in mutual subserviency to another is greatest, and the deviation from the archetype is in the same degree. The rectification of the mistakes and the acquisition of a more catholic feeling towards the study are gained by pursuing the broader high-road of organic nature, where those forms are offered to our contemplation in which vegetative uniformity most prevails, and the archetype is least obscured by purposive adaptations.

If therefore we find in that class which best displays the conditions for solving the problem immediately before us, that the connections of the scapular arch are such as to complete a typical segment, which otherwise would be abnormal by defect, we must conclude that the type is here adhered to; and that, although these connections are abrogated in all the other Vertebrate classes, they, nevertheless, are the 'instantiæ deviantes,' and are exceptions in regard to the rule of the archetype, notwithstanding the actual numerical superiority of the instances.

And the latter fact leads us to another consideration. This superiority was not always such as it now is. Time

* Novum Organum Scientiarum, lib. ii. Aph. xxix.

was when fishes were the sole representatives of the Vertebrate subkingdom in this planet. During the long periods antecedent to the formation of the coal-measures, the vertebrate type was exclusively manifested by forms in the great majority of which the scapular arch was articulated to the occiput. Subsequent changes in our planet have heightened and varied the conditions of animal existence, but the primitive pattern of the skeleton may be discerned beneath all the superinduced modifications.

We perceive a return to it, as it were, in the early phases of development of the highest organized of the actually existing species, or we ought rather to say, that development starts from the old point; and thus, in regard to the scapula, we can explain the constancy of its first appearance close to the head, whether in the human embryo or in that of the swan, and also its vertical position to the axis of the spinal column, by its general homology as the rib or 'pleurapophysis' of the occipital vertebra.

We observe, as might naturally be expected, that its degree of displacement is least in those air-breathing Vertebrata that make the nearest approach to fishes: whether in general structure, as *e. g.* the siren and amphiuma, or in outward form, as *e. g.* the Cetacea. In comparing the crocodile's skeleton (fig. 3. Pl. I.) with that of the fish, the chief modification that distinguishes the occipital segment from its homologue in the fish, is the absence of its attached hæmal arch. We recognise, however, the special homologues of the chief piscine constituents of that arch in 51 and 52; but the upper or suprascapular piece (50) retains, in connection with the loss of its proximal or cranial articulations, its cartilaginous state, and is not shown in fig. 3: the scapula (51) is ossified, as is likewise the coracoid (52), the lower end of which is separated from its fellow by the interposition of a median, symmetrical, partially ossified piece called 'episternum' (*hs*). The power of recognising the special homologies of 50, 51, and 52 in the

crocodile, with the similarly numbered constituents of the arch H 1 in fishes (fig. 2), though masked not only by modifications of form and proportion but even of very substance, as in the case of 50, depends upon the circumstance of these bones constituting the same essential element of the archetypal skeleton: for although in the present instance there is superadded to the adaptive modifications above-cited the rarer one of altered connections, Cuvier does not hesitate to give the same names (suprascapulaire) to 50 and (scapulaire) to 51, in both fish and crocodile: but he did not perceive or admit that the narrower relations of special homology were a result of, and necessarily included in, the wider law of general homology. According to the view which I am attempting to establish and illustrate, we discern in 50 and 51 a teleologically compound *pleurapophysis*, in 52 a *hæmapophysis*, and in *hs* the *hæmal spine*, completing the hæmal arch.

The general relations of the scapulo-coracoid arch to a hæmal or costal one was recognised, as I have already observed, by Oken. This philosopher, having observed the free cervical ribs in a specimen of the *Lacerta apoda* (*Pseudopus*), deemed them representatives of the scapula, and this bone to be, in other animals, the coalesced homologues of the cervical pleurapophyses*. In no animal are the conditions for testing this question so favourable and obvious as in the crocodile (fig. 3. Pl. I.): not only do cervical ribs coexist with the scapulo-coracoid arch, but they are of unusual length and are developed from the atlas as well as from each succeeding cervical vertebra: we can

* "Auch die Scapula nicht *ein* Knochen, sondern wenigstens eine aus fünf Halsrippen zusammengeflossene Platte ist."—*Programm über die Bedeutung der Schädelknochen*, 4to, 1807, p. 16. He reproduces the same idea of the general homology of the scapula in the 'Lehrbuch der Natur-philosophie,' 1843, p. 331, ¶ 2381. Carus also regards the scapulo-coracoid arch as the reunion of several (at least three) protovertebral arches of the trunk-segments. 'Urtheilen des Knochen und Schalen gerustes,' fol. 1828.

also trace them beyond the thorax to the sacrum, and throughout a great part of the caudal region, as the sutures of the apparently long transverse processes of the coccygeal vertebræ demonstrate in the young animal; the lumbar pleurapophyses being manifested at the same period as cartilaginous appendages to the ends of the long diapophyses.

The scapulo-coracoid arch (51,52), both elements of which retain the form of strong and thick vertebral and sternal ribs in the crocodile, is applied in the skeleton of that animal over the anterior thoracic hæmal arches. Viewed as a more robust hæmal arch, it is obviously out of place in reference to the rest of its vertebral segment. If we seek to determine that segment by the mode in which we restore to their centrums the less displaced neural arches in the sacrum of the bird (fig. 10, *n* 1–*n* 4), we proceed to examine the vertebræ before and behind the displaced arch with the view to discover the one which needs it in order to be made typically complete. Finding no centrum and neural arch without its pleurapophyses from the scapula to the pelvis, we give up our search in that direction; and in the opposite direction we find no vertebra without its ribs until we reach the occiput: there we have centrum and neural arch, with coalesced parapophyses—the elements answering to those included in the arch fig. 7, c, *n*, *p*, *ns*, but without the inverted arch *pl*, *h*, *hs*; which arch can only be supplied, without destroying the typical completeness of antecedent cranial segments, by a restoration of the bones 51–52, fig. 3, Pl. I. to the place which they naturally occupy in the skeleton of the fish (fig. 2). And since anatomists are generally agreed to regard the bones 51–52 in the crocodile (Pl. I. fig. 3) as specially homologous with those so numbered in the fish (*ib.* fig. 2), we must conclude that they are likewise homologous in a higher sense; that in fig. 2 the scapulo-coracoid arch is in its natural or typical position, whereas in the crocodile it has been displaced for a special purpose. Thus, agreeably with a general

principle, we perceive that as the lower vertebrate animal illustrates the closer adhesion to the archetype by the natural articulation of the scapulo-coracoid arch to the occiput, so the higher vertebrate manifests the superior influence of the antagonising power of adaptive modification by the removal of that arch from its proper segment.

The scapula retains the more common cylindrical long and slender rib-like form of the pleurapophysis in the chelonian reptiles, where, from the greater length of the neck, it has retrograded further than in the crocodile from its proper centrum, and is placed not upon, but within, an anterior thoracic hæmal arch, by virtue of the great expansion to which the pleurapophysis of that arch has been subject. Here the rib has become a broad and flat bone*, whilst the scapula has retained its primitive rib-like shape.

If the arguments founded upon the relations of the scapulo-coracoid arch to the segments of the skeleton in osseous fishes and crocodilians be admitted to sustain the conclusion here drawn from them, that arch must be held to form the hæmal complement of the occipital vertebra in all animals.

Bojanus, in illustrating his vertebral theory of the skull by the osteology of the *Emys Europæa*, thus defines the

"VERTEBRA OCCIPITALIS, SIVE CAPITIS PRIMA.

"Basis occipitis, seu *corpus* hujus vertebræ,

"Pars lateralis occipitis, sive *arcus*,

"Crista occipitalis, *processus spinosi* loco,

"Cornu majus hyoidis, *costæ vertebræ* occipitalis comparandum†."

He adds a dotted outline of the hyoid arch to complete the *vertebra occipitalis*, in tab. xii. fig. 32, B. 1 of his beautiful Monograph.

* By what process this metamorphosis is effected I have explained in a Memoir read before the Royal Society, January 18th, 1849.

† Anatome Testudinis Europææ, fol. 1819, p. 44.

Supposing the special homology of the middle cornua of the hyoid of the chelonian, so represented and compared to ribs by Bojanus, with the stylo-, epi- and cerato-hyals of the fish (Pl. I. fig. 2, 38, 39, 40) to have been correct, which the metamorphoses of the hyoid and branchial arches in the batrachians disprove, the singular and highly interesting change of position as well as shape of the true ceratohyals, during the same metamorphosis, prepares us to expect a retrogradation of the hyoid arch in respect to its proper centrum, in the skulls of the air-breathing vertebrates. In the young tadpole the thick cartilaginous hyoidean arch* is suspended, as in fishes, from the tympanic pedicle: the slender hyoidean arch of the mature frog is suspended from the petrosal capsule†. The mandibular arch has, also, receded; and the scapular arch, which, at its first appearance, was in close connection with the occiput, further retrogrades in the progress of the metamorphosis to the place where we find it in the skeleton of the adult frog.

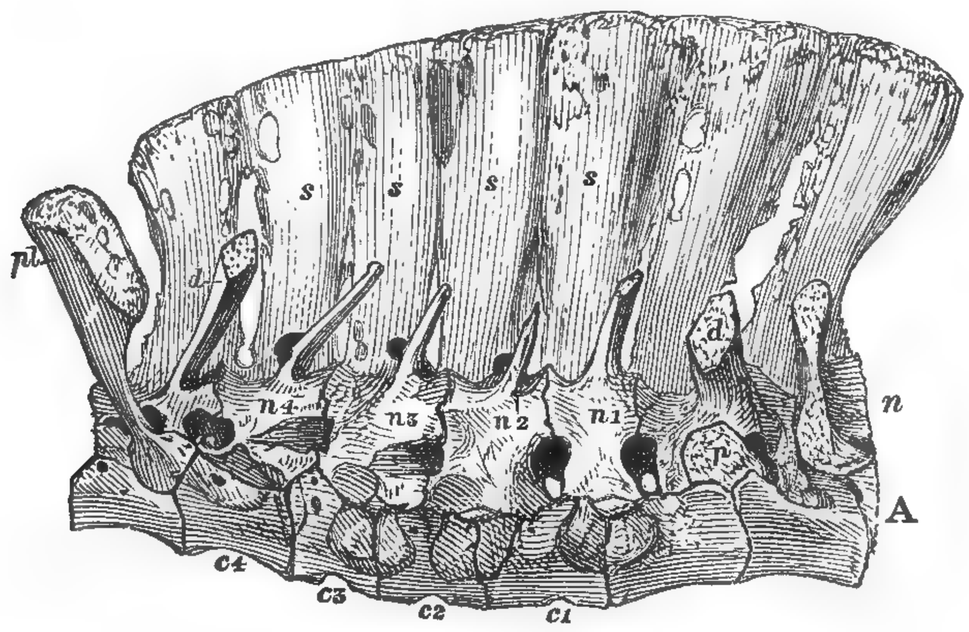
The argument, therefore, may be summed up as follows. The position of the pleurapophyses in the human thorax and that of most mammals; and the position of the neurapophyses in the dorsal vertebræ of chelonians and in the sacral vertebræ of dinosaurians and birds, show that a change of relative position in respect of other elements of the same vertebra may be one of the adaptive modifications to which even the most constant and important of those elements are subject. Instead of viewing such shifted arches as primary and independent constituents of the skeleton, we recognise them as secondary and derivative parts of a natural segment or whole, and we trace their relation to the stationary elements—the centrums of the primary vertebral segments.

* Cuvier, Ossem. Foss. v. pt. ii. pl. 24, fig. 23 *a*.

† *Ib.* fig. 27 *a*:—an intermediate stage is shown at fig. 25. Dugés and Reichert confirm and further illustrate this change of position of the hyoidean arch.

Thus, commencing, for example, with the anterior of the sacral vertebræ of the ostrich, A in fig. 10, we observe that,

Fig. 10.



Seven sacral vertebræ of a young ostrich (*Struthio camelus*).

besides supporting its own neural arch *n*, it bears a small portion of that of the next vertebra: the third neural arch (*n* 1) has encroached further upon the centrum of the vertebra in advance; and thus, in respect to the neural arch (*n* 2), if it were viewed with the centrums, *c* 2 and *c* 1, upon which it equally rests, apart from the rest of the sacrum, it would appear to appertain equally to either, and be referable to the one in preference to the other quite gratuitously, to all appearance. Nevertheless *n* 2 is proved, by the intermediate changes in antecedent neural arches, to belong actually, and in no merely ideal or transcendental sense, to *c* 2 altogether, and not to the segment of which *c* 1 is the centrum; and in tracing the modifications of those sacral vertebræ which follow *c* 2, we find *n* 4 to have regained nearly the whole of its centrum, *c* 4, and the normal relations of the elements are quite restored in the succeeding vertebra.

Now let us suppose the habits of the species to have required a more extensive displacement of the arch (*n* 2) and its appendages: if its formal characters as a neural arch were still retained beneath the adaptive development superadded to the adaptive dislocation, and if the segments be-

fore and behind the centrum *c* 2 were found complete, and that centrum alone wanting its neural arch; would the mere degree of modification in respect of relative position nullify the conclusion that the shifted arch appertained to such incomplete segment, and forbid that restoration to the typical condition, which no anatomist, it is presumed, will dispute in the case of *n* 2, *c* 2, fig. 10?

The anthropotomist, by his mode of counting and defining the dorsal vertebræ and ribs, admits, unconsciously perhaps, the important principle in general homology for which we are contending, and which, pursued to its legitimate consequences and further applied, demonstrates that the scapula is the modified rib of that centrum and neural arch which he calls the 'occipital bone,' and that the change of place which chiefly masks that relation (for a very elementary acquaintance with comparative anatomy shows how little mere form and proportion affect the homological characters of bones) differs only in extent and not in kind from the modification which makes a minor amount of comparative observation requisite in order to determine the relation of the shifted dorsal rib to its proper centrum.

With reference, therefore, to the occipital vertebra of the crocodile, if the comparatively well-developed and permanently distinct ribs of all the cervical vertebræ prove the scapular arch to belong to none of those segments, and, if it be wanting to complete the occipital segment, which it actually does complete in fishes, then the same conclusion must apply to the same arch in other animals, and we must regard the occipital vertebra of the tortoise as completed below by its scapulo-coracoid arch, and not, as Bojanus supposed, by its hyoidean arch *.

* Geoffroy St. Hilaire selected the opercular and subopercular bones to form the inverted arch of his seventh (occipital) cranial vertebra ('Tableau de la Composition de la Tête osseuse de l'Homme et des Animaux,' cited in Cuvier's 'Histoire de Poissons,' tom. i. p. 230. See

The facts and arguments that determine the nature of the hæmal arch of the occipital vertebra in reptiles equally apply to that in the bird (see fig. 4, 51, 52, Pl. I.). The extent of its displacement, it is true, has been greater: not seven only, but seven and twenty vertebræ may intervene between its actual position and that of the rest of its proper segment. But this difference of extent of displacement ought no more to hide the true relationship of the scapulo-coracoid arch to its proper position and typical segment in the skeleton, than the jugular position of the ventral fins of a fish (Pl. I. fig. 2, v″) prevents the ichthyologist from determining their nature and consequently their proper position in relation to the archetype skeleton.

In Mammalia we find the scapula retaining its primitive vertical position and much of its elongated narrow form in the low ovoviviparous monotremes; and the arch in them is completed by the coracoid. We observe the scapula long and slender in the mole (fig. 2, 51); but in most of the class it is developed into a broad quadrate or triangular plate, with outstanding exogenous processes called 'spine' and 'acromion.' The hæmapophysial element is also reduced to an appendage, as in the false ribs at the back part of the thorax, and coalesces as a process (Pl. I. fig. 4, 52) with the pleurapophysis (51). In many mammals and in man, the arch is completed by the pair of bones called clavicles (Pl. I. fig. 6, 58) which coexist with the coracoids in most birds and reptiles. I have elsewhere adduced the facts and arguments which show that the bone 58, figs. 4, 5 & 6, Pl. I., is the special homologue of the bone 58 in the fish (fig. 2, 51 & 52)*: and its anterior position to the coracoid in the air-breathing Vertebrata is no valid

also the Table III. and note 11 in my Work 'On the Archetype,' &c. p. 172), and took no account of the instructive natural connections and relative position of the hyoidean and scapular arches in fishes.

* 'On the Archetype and Homologies of the Vertebrate Skeleton,' pp. 19, 99, 133.

argument against the determination, since in these we have shown that the true scapular arch is displaced backwards. The parallelism of the clavicles with the coracoids, and their inferior convergence, indicate their serial homology with the coracoids, and consequently their general homology as 'hæmapophyses'; and I regard the clavicle in its relations to the vertebrate archetype (Pl. I. fig. 1), as the displaced hæmapophysial element of the atlas, to which segment its true relative position is shown in the same low organized class (fig. 2, 58) in which the typical position of the scapular arch is likewise retained.

Having thus traced out and determined the nature, 'bedeutung' or general homology of the scapular arch, the next step, in regard to the limb appended to it, is plain and easy. We saw that the typical segment of the vertebrate skeleton (p. 42, fig. 7) was occasionally complicated by an appendage (*a*) developed from each side of the hæmal arch, serving to attach that arch to the next in succession in the thorax of birds (*a*, *p*); but diverging into the flesh and adding to the leverage of the locomotive powers in the abdomen of fishes (Pl. I. fig. 2, *a*, *a*). The pectoral extremities exhibit varied developments of this appendage; but, if our determination of their general homology be the true one, we ought to trace them under progressive stages of reduction and simplification to their primitive or archetypal character.

Already, in the class of Birds, we find the diverging appendages of the scapulo-coracoid arch of the apteryx (fig. 9, 53–57, *a*) reduced in bulk nearly to the dimensions of those of the thoracic-costal arches (*a*, *a*), but projecting into the flesh like the costal appendages of fishes; and, being a longer ray, protruding its extremity beyond the tegumentary surface, but to so short an extent that the whole of this monodactyle limb or rudimental wing is concealed by the plumage.

The proportion of the fore-limb to the supporting arch

in the proteus and amphiuma (Pl. I. fig. 8, 53–57, *a*) is hardly greater than that of the ray-like appendage to the abdominal rib in many fishes.

In the lepidosiren (*ib.* fig. 7, 53–57, *a*) we actually find the diverging appendage of the scapular arch retaining its elementary form of the ray, and differing only by its segmentation and relative length from its serial homologues (*ib.* fig. 2, *a* *a*) in the succeeding segments of the skeleton of better ossified fishes. But by virtue of its elongation it extends beyond the surface of the body, and carries with it a sheath of the integument.

In the view of the Archetype skeleton (Pl. I. fig. 1), the pectoral limb (53–57, *a*) is represented under this form as the diverging appendage of the fourth or occipital hæmal arch (50, 51, 52, 52′), and its serial homology with the shorter appendages (*a*, *a*) of the succeeding arches is unmistakeable.

If then the diverging rays or appendages of the thoracic and abdominal vertebræ of fishes (fig. 2, *a*, *a*), of reptiles (fig. 3, *a*, *a*), and of birds (fig. 4, *a*, *a*), be serial repetitions of the more developed appendage of the scapulo-coracoid arch, they must be 'rudimental limbs,' future possible or potential arms, legs, wings or feet.

To become recognised specially as a 'limb,' it needs only that the diverging appendage carry out beyond the surface a fold or sheath of the integument, which it may be able by its muscles to move and make react upon the ambient medium or supporting surface. Hence the simple filamentary ventral appendages of the lepidosiren and the blenny are acknowledged by Naturalists as hinder limbs. In Zoology, however, not more than two pairs of limbs are recognised in the Vertebrate series. But with our present knowledge of the nature of limbs, we are stimulated to inquire whether there be no other diverging appendages of hæmal arches similarly developed and deserving that name?

If we examine the segments of the skeleton in advance of the occipital one, which are represented by their inferior or hæmal arches in the lepidosiren *, we shall find that each of them developes its pair of appendages (23, 34, 37) : that (37) from the hyoid (parieto-hæmal) arch projects freely outwards as a simple osseous unsegmented ray : that (34) from the tympano-maxillary (fronto-hæmal) arch has a like form and condition. The diverging appendage of the maxillary (naso-hæmal arch) is anchylosed as a (pterygoid) process, and repeats the function of the costal appendages in birds by attaching the arch from which it diverges to the next in succession. The free moveable appendages of the tympanic and hyoid arches carry out with them a fold of integument; but, like the ventral and pectoral fins of the lump-fish (*Cyclopterus*), they combine to support the same fold or rudimental fin, which is denominated the 'operculum'; but this is essentially a limb, or rather two cephalic limbs conjoined, which, in fact, are specially distinguished in ichthyology as the 'opercular' and 'branchiostegal' flaps.

An osseous fish, therefore, of the type of that the skeleton of which is represented in Pl. I. fig. 2, is an 'octopod,' and six of its limbs belong to the head. With regard to the third pair, which are more especially organized for locomotion, whatever be their ultimate development and destination, they always first appear in the simple form in which they are permanently arrested in the lepidosiren, viz. as an unbranched ray. Development simply augments its length and the number of its segments in the lepidosiren : in other fishes the jointed ray is multiplied : sometimes a segment is modified between the terminal rays and the supporting arch, which may be recognised as a carpus (*Lophius* †): sometimes a second seg-

* Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals, 8vo, 1846, p. 79, fig. 27, 19, 32, 40.

† *Ib.* p. 121, fig. 40, 56.

ment is interposed between the 'carpus' and the arch, which may be recognised as the 'antibrachium' (Pl. I. fig. 2, 54, 55): but the development of definite segments in the longitudinal direction of the limb does not go beyond this point in fishes. Far otherwise, however, is it in respect of development in breadth; multiplication of digital rays is the characteristic type of the pectoral extremity in the piscine class, and reaches its maximum in the species which have accordingly received the emphatic denomination of 'Ray-fishes' (*Raiidæ*). And this mode of complication of the pectoral member by vegetative repetition of like parts, is a striking and instructive instance of the special divergence of the piscine branch from the common Vertebrate stem.

In order to follow the development of the diverging appendage of the occipital hæmal arch through other ramifications of that stem, we must retrace our steps to the species in which it retains its embryonic state and represents its archetypal character. The first step in development from the primitive type of the pectoral ray of the lepidosiren is made by the *Amphiuma didactylum* (Pl. I. fig. 8). The hæmal arch is detached from the neural arch, and slightly displaced backwards; but the pleurapophysis (*pl*, 51) retains its simple rib-like form and position, slightly inclining outwards below from the vertical line. The hæmapophyses (*h*, 52) do not pass beyond the state of gristle, but are much expanded: they resemble in their histological condition their homotypes, called 'cartilages of the ribs,' in the thorax of man. If the study of the essential nature of the detached inverted arch so formed had been begun at this point and compared with that of the Vertebrates lower in the scale, no doubt, I apprehend, would have been entertained as to the detachment of such hæmal arch in the amphiuma being a deviation from type, and its attachment to the rest of its segment in the lepidosiren and osseous fishes as being a retention of the typical struc-

ture: this condition would have been in point of fact the rule, and the other the exception.

So likewise with respect to the diverging appendages, *a a*, of the occipito-hæmal arch of the amphiuma: if the anatomist had observed them with a previous knowledge only of the lepidosiren and other fishes, the bones 54, 55 and 57 would doubtless have been regarded and described only as bifid segments of the primitive simple ray. But the parts having been originally studied from a higher point in the animal series, where the homologues of those segments by virtue of their special developments in adaptation to special functions had obtained special names, those names were naturally transferred to their simplified homologues in the appendage recognised as the anterior limb or extremity of the amphiuma: the proximal single segment 53 was described as 'humerus,' the ossified divisions of the next segment as 'radius' and 'ulna' (54 and 55), the terminal bifurcation (57) as the 'digits.' This extreme instance of the exemplification from 'special homology' of the unity of the plan upon which the limbs of the vertebrate animals have been constructed is a perfectly true one.

Cuvier has most accurately assigned their special names to each of the parts of the fore-limb of the amphiuma in his celebrated memoir*. All that I would ask of the most devoted disciple of the school of 'positive facts' is to reciprocate; to grant the inference as to the signification of the parts arrived at by their study in the ascending route of inquiry, which the homologist is ready to give to the determinations of the special character of the parts which have been obtained by comparisons pursued descensively from man: in other words, to admit that the whole (53–57)

* "Dans ces deux figures *a* est l'*omoplate*, *b* les plaques sternales cartilagineuses formées probablement des *os coracoïdiens*; *c* l'*humerus*, suivi du *cubitus* et du *radius* qui portent un *carpe* cartilagineux et deux os *metacarpiens* et *phalangiens* osseux." Mémoire lu à l'Académie des Sciences, le 13 Novembre 1826, p. 15.

in the amphiuma (fig. 7) may be the homologue of the ray (53–57) in the lepidosiren (fig. 6); that this may answer to the ray (53–57 *a*) in the fourth segment of the archetype (fig. 1); and that such ray is repeated in the diverging appendages, *a a*, of the succeeding segments of the skeleton: whereby he will be led to the recognition of the essential nature of the limbs as developed diverging appendages of the hæmal arches of vertebræ, and the fore-limbs as being such appendages of the occipital vertebra*. The facts are not less 'positive' than they were before, only they cease to be empirical and become intelligible.

I need not trespass further on the time of this distinguished audience, by adding instances of the complication and concomitant powers of these appendages to those that have already been illustrated at the commencement of the present discourse; I will only repeat, that the adaptive developments of the radiated appendage of the occipital hæmal arch reach their maximum in man, and the distal segment of the appendage constitutes in him an organ which the greatest of ancient philosophers has defined as the "fit instrument of the rational soul;" and which an eminent modern physiologist has described "as belonging exclusively to man—as the part to which the whole frame must conform†." And these expressions give no exaggerated

* The want of connection of a peripheral piece, at its peripheral end or border, appears to be one condition of its greater extent of variety of form and proportion than in the more central pieces of a natural segment. There is nothing to restrain its luxuriant development from a simple spine to a plate, to a divided plate with intercalations, &c., or to a lengthened segmented ray bifurcating into additional segments with indefinite modifications of these. Always, however, it is to be remembered that the polarising forces which tend to shoot out particle upon particle after the pattern of dendritic corals, lichens or crystals, are so controlled by the antagonising principle of adaptation, that the radiating growth is always checked at that stage and guided to that form which is best suited to the needs and habits and sphere of life of the species.

† Sir Charles Bell, Bridgewater Treatise, 1833, pp. 16, 18.
Μόνον δὲ καὶ ἀμφιδέξιον γίγνεται τῶν ἄλλων ζώων ἄνθρωπος.—Aristotle.

idea of the exquisite mechanism and adjustment of its parts.

It is no mere transcendental dream, but true knowledge and legitimate fruit of inductive research, that clear insight into the essential nature of the organ, which is acquired by tracing it step by step from the unbranched pectoral ray of the lepidosiren to the equally small and slender but bifid pectoral ray of the amphiuma, thence to the similar but trifid ray of the proteus, and through the progressively superadded structures and perfections in higher reptiles and in mammals. If the special homology of each part of the diverging appendage and its supporting arch are recognisable from Man to the fish, shall we close the mind's eye to the evidences of that higher law of archetypal conformity on which the very power of tracing the lower and more special correspondences depend?

Until the alleged facts (pp. 50, 53) are disproved, demonstrating change of position to be one of the modifications by which parts of a natural and recognisable endoskeletal segment are adapted to special offices, and until the conclusions (pp. 54, 58) deduced from those facts are shown to be fallacious, I must retain the conviction that, in their relation to the vertebrate archetype, the human hands and arms are parts of the head—diverging appendages of the costal or hæmal arch of the occipital segment of the skull*.

* As another example of the new light and interest which a knowledge of general homology gives to the facts of abnormal anatomy in the human species, I may cite the remarkable case described by Sir C. Bell (*op. cit.* p. 52), of the boy 'born without arms,'—'but who had clavicles and scapulæ.' Here development was arrested at the point at which it is normal in the *Anguis*, *Pseudopus*, and some other limbless and snake-like lizards. The usual predominating development of the scapular appendage has bred so prevalent an idea of the subordinate character of the supporting arch, that the existence of the arch minus the appendage, is adverted to not without a note of surprise in the above-cited and other excellent works. General homology, however, teaches that a vertebral arch is a more constant and important part than its appendages; and, that, being anterior in the order of develop-

Having thus arrived at a solution of the question mooted at the outset of the present Discourse, viz. the signification, 'bedeutung' or general homology of locomotive members, and of the pectoral pair in particular, little needs to be added in respect of the pelvic pair of limbs.

When a bone in the skeleton of a dog, a horse, a mole, and a platypus, is proved to be the same or answerable bone to the one called 'scapula' in man, and is called by the same name; and when the answerable bone can be traced through birds, reptiles and fishes, where it is similarly recognised and indicated,—determined, in short, to be the namesake or 'homologue' of the human scapula; it follows, that, whatever other or higher proposition respecting the nature of that bone and its relations to the fundamental pattern of the vertebrate skeleton can be demonstrated by the sum of its characters in all applies individually to every form of the bone: and whatever element of the typical segment of the skeleton it may be recognised to be in an instance where the typical characters are best retained, such conclusion equally applies to the instances in which it is most metamorphosed. In other words, when the general homology of a bone is determined in any one species, the same is proved of its special homologues in every other species. If the scapula of the lepidosiren is the rib of the occipital vertebra, every other scapula must be the same element.

ment, it may be expected, in cases where development is arrested, whether normally in accordance with the nature of the species, or abnormally as an individual defect, to be present when the diverging appendages are absent. Sir Charles Bell, well recognising the primary function of the modified occipital rib in relation to breathing, observes, in reference to the above-cited case, "We would do well to remember this double office of the scapula and its muscles, that, whilst it is the very foundation of the bones of the upper extremity, and never wanting in any animal that has the most remote resemblance to an arm, it is the centre and point d'appui of the muscles of respiration, and acts in that capacity where there are no extremities at all!"—P. 52.

So, likewise, when a bone in a given natural segment of the skeleton is demonstrated to be answerable to another bone in another natural segment of the same skeleton, whatever higher homological proposition may be demonstrated of the one must apply to the other and to all its serial homologues, *i. e.* to all the bones that have been shown to stand in the same relations to their respective segments. The comprehension of these propositions will be facilitated by tracing the bones that have the same kind of marking, from segment to segment, in the diagrams of the skeletons in Pl. I.

No anatomist, I presume, could doubt or would contravene so plain a proposition as that the frontal bone or bones in their part of the skull repeat the general relations of the parietal bone or bones in their part, and those of the supraoccipital bone in its part of the skull; or that the basioccipital in its segment repeated the essential characters of the basisphenoid in the next segment.

Whatever element, therefore, of the typical segment the supraoccipital is demonstrated to be, the same must be true, not only of the supraoccipital in all other animals, but of the parietals and frontals in the succeeding segments of the same animal. And whatever element the basioccipital is demonstrated to be in its segment, the basisphenoid must be that element in the succeeding segment. In other words, when parts are demonstrated to be 'homotypes' or serial homologues, a general homology proved of one applies to all*.

A due appreciation of these rigorous deductions will leave no difficulty in dealing with the general homology of the hinder or pelvic limbs.

Anatomists with one consent admit that the ilium is the

* The terms 'general,' 'special,' and 'serial homology,' are explained and exemplified in my "Lectures on the Comparative Anatomy and Physiology of the Vertebrata," p. 48, and 'On the Archetype of the Vertebrate Skeleton,' p. 7.

homotype of the scapula; in other words, is the answerable bone in the series of segments of the same skeleton: few, if any, doubt, and none with reason, that the ischium is the homotype of the coracoid, and the pubis of the clavicle. The ilium must therefore be, like the scapula, a 'pleurapophysis,' and the ischium and pubis, like the coracoid and clavicle, must be 'hæmapophyses'; for whether the serial homology just enunciated in regard to the latter bones be accepted or inverted, and the pubis be viewed as the homotype of the clavicle or coracoid, matters not; they are the same elements of the hæmal arch in the abstract; their general homology is, therefore, the same.

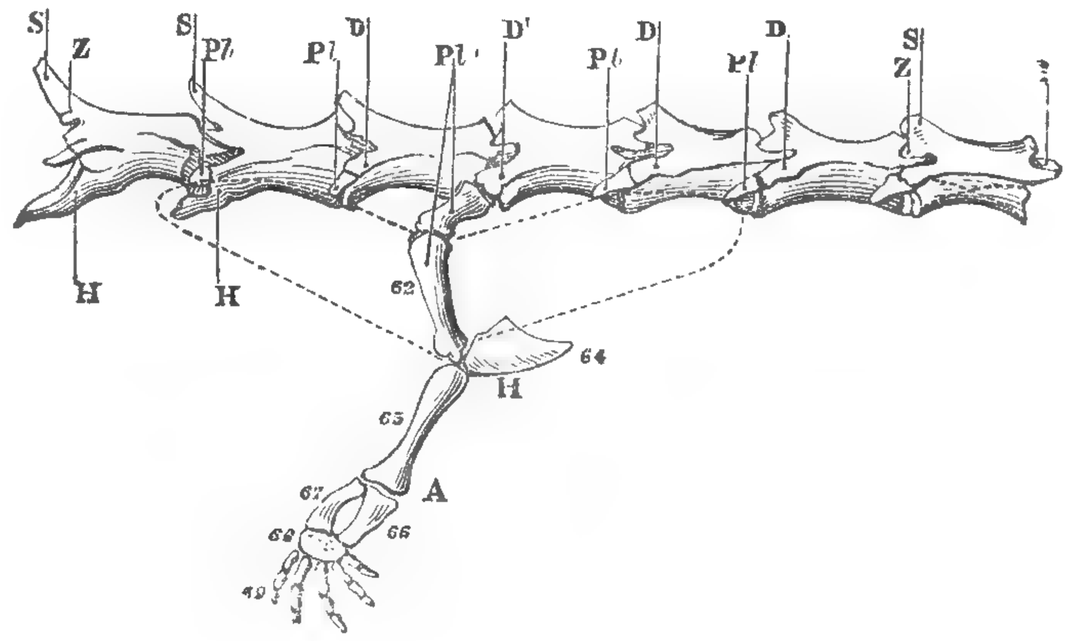
The serial homology of the pectoral and pelvic extremities has been so fully discussed, that no more need be added on that head to prove their general homology. If the pectoral members have been demonstrated to be developments of the diverging appendages of the hæmal arch, the pelvic members must necessarily be the same elements of the typical vertebra.

This conclusion as to the general homology of the hind-limbs would, however, have been arrived at if the study of the Nature of Limbs had been commenced with them, and had been illustrated by their morphological and developmental characters, independently of the light reflected from serial homology. But as it may serve to establish confidence in the truth of the evidence by which such generalizations are arrived at, I will briefly adduce some of the more striking facts or links in that independent chain of reasoning.

The most simple and elementary condition of the complete and normally connected pelvic arch and appendages is found in the lowest forms of crawling reptiles, viz. the perennibranchiate *Batrachia*. Here is a side view of the parts in the *Menopoma* (fig. 11), and fig. 10 in Pl. I. gives a direct front-view of them in the *Proteus*. In fig. 11 the three anterior vertebræ which answer in position to the

'lumbar' vertebræ in Pl. I. fig. 3, differ chiefly in having pleurapophyses (P*l*) articulated and not anchylosed to the

Fig. 11.



Pelvic vertebra and appendage with contiguous vertebræ (Menopome).

ends of the diapophyses (D); but the ribs are rudimental, and the archetypal segment is departed from by defect of the hæmal arch. In the next vertebra the diapophysis (D′) is thickened, and the pleurapophysis (P*l*) elongated and divided into two parts like the occipital pleurapophysis in the fish (Pl. I. fig. 2, 50, 51): and the second rib-like piece (62, fig. 11) is joined by its lower end to a broad partially ossified cartilage (64), the hæmapophysis, which meets and joins its fellow, completing a hæmal arch and restoring the vertebra in question to the typical character. A radiated appendage, A, moreover, diverges on each side from the articulation between 62 and 64, and forms the hind-limb. Now the special homology of this limb with the undivided filamentary appendage similarly situated in the lepidosiren (Pl. I. fig. 9) and with the ventral fins of fishes, in the descending series, and with the hind-limb of other reptiles, of birds and of mammals in the ascending series, is unmistakeable, and, I believe, is generally admitted: so that comparative anatomists have not hesitated to call the rib-like bone (62) 'ilium,' and the cartilage (64) 'ischium' or 'pubis' in the menopome.

The correspondence of the segment of the endoskeleton in the menopome D′, P*l*′, H, A, with the typical vertebra, as illustrated by fig. 7, p. 42, is such, that any other explanation of its essential nature than as a representative or repetition of such fully-developed segment or vertebra, would be plainly contrary to nature. The chief modification has its seat in the most peripheral part, viz. the appendage A, as compared with its simple homologue in the thoracic segment of the bird (fig. 7, *a*). If 62 and 64, fig. 11, are to be regarded as strangers to the vertebral system, new parts introduced for special purposes, and not as normal elements modified for special purposes, I am at a loss to know on what principles, or by what series of comparisons we can ever hope to attain to the higher generalizations of anatomy, or discover the pattern after which the vertebrate forms have been constructed.

It may be said that the arch which they constitute performs a new function, inasmuch as it sustains a locomotive limb which reacts upon the ground. But this new function arises in the menopome, rather out of the modifications of the appendage than of the arch itself. In so far as the mere support of the appendage is concerned, the inverted or hæmal arch (P*l*′, H) performs no new function, but one which is common to such arches in the thorax of birds, and to the less completely ossified homologous arches in the abdomen of fishes, where moreover the simple diverging appendages (Pl. I. fig. 2, *a*, *a*) do give attachment to the muscles of locomotion.

Comparing, then, the hæmal arch in question with that of the typical vertebra (fig. 7, p. 42), we find that, like the scapulo-coracoid arch in fishes (Pl. I. fig. 2, and fig. 7, 50, 51, 52), its parts are open to two interpretations. The upper piece of P*l*′ may be the whole pleurapophysis, the lower (62) the hæmapophysis, and the part, 64, the half of an expanded and bifid hæmal spine: or P*l*′ with 62 may be two portions of a teleologically compound pleurapophysis, and 64

the hæmapophysis, which would join with its fellow without, or with a mere rudiment of, a hæmal spine intervening. From the analogy of the scapulo-coracoid arch in fishes, which is proved by its modifications in higher animals to want the hæmal spine, we might infer that such was the condition and true interpretation of the correspondingly simple pelvic arch under consideration, and the inference is confirmed by the undivided condition of the pleurapophysis or 'ilium' in the proteus (Pl. I. fig. 10, 62), as well as by the position from which the appendage or limb diverges. But the general relation of this arch to the hæmal one of the typical segment is not affected by the alternative.

In ascending from the proteus and menopome to the crocodile (Pl. I. fig. 3), we find the homologue of 62 broader than it is long, and articulated to the thickened proximal portions of the pleurapophyses of two vertebræ; and we observe, likewise, the pelvic arch completed below by two pairs of hæmapophyses: for the anterior pair the name of 'ossa pubis' is retained; for the posterior pair that of 'ischia.' In general homology these bones complete, as hæmapophyses, the two vertebral segments modified to form the sacrum of the crocodile; and the intermediate connecting piece (ilium) might be interpreted, as either the confluent distal portions of the pleurapophyses of both vertebræ, or as an expansion of one such portion, answering to 62 in the menopome, and intruding itself between the stunted pleurapophysis and distant hæmapophysis of the other sacral vertebra in the crocodile.

The doubt thus left in the prosecution of the inquiry by the successive steps of special homology is resolved by the light of serial homology. The ilium is the homotype of the scapula; it parallels the scapula in the nature and extent of its morphological modifications; and, since the scapula under its extremest expansion is proved to be the development of one and the same element, viz. the lower portion of the divided occipital pleurapophysis in the fish, so

likewise must the broadest ilium be considered to be the development of the same portion of one pelvic pleurapophysis. Its broad expanded modification is its common morphological character in Mammalia; and its position becomes less vertical than in reptiles, and more oblique; and in both these particulars it resembles the scapula. In Plate I. 62 shows its common form in quadrupeds, fig. 5, and 62 in fig. 6 its still broader proportions in man, in relation to the extent of surface required by the muscles that sustain the upright trunk upon the diverging appendage of the arch.

The second sacral vertebra in man is complete; but its pleurapophysis is in two pieces, as in the menopome: the proximal piece coalesces with the neural arch and forms the so-called 'transverse process' of the vertebra; the distal or lower portion is expanded to form the so-called 'ilium' (62). The hæmapophysis (63) coalesces with that of the preceding vertebra (64), and with its own pleurapophysis (62).

The first sacral vertebra has its hæmapophysis (64, called 'pubis') ossified, but separated from its proper pleurapophysis by the expanded (iliac) portion of that of the succeeding vertebra (62), with which it coalesces, as well as with the succeeding hæmapophysis (63, 'ischium'). The short and thick pleurapophyses of the third sacral vertebra also articulate, in the adult, with the expanded distal portion of those of the second sacral vertebra; but these (iliac bones) are restricted in infancy and early childhood to their connections with the first and second sacral vertebræ, which connections are permanent in most reptiles.

In the bird the modification of the vertebral segments at the posterior region of the trunk in relation to the transference of the whole weight of the body and fore-limbs (wings) upon the hind-limbs, is greater and more extensive than in man, and the essential nature of the pelvic arch is still more masked. By the extreme expansion of the

element 62, fig. 4, Pl. I., it is brought into connection with the homologous stunted or proximal ends of pleurapophyses of several contiguous segments, besides its own proximal piece, in the manner indicated by the dotted line in the menopome (fig. 11, p. 74).

Now, if the ilium, so expanded, were interpreted as the coalesced complementary portions of all the short pleurapophyses with which it articulates, its nature would be very similar to that which Oken has attributed to the scapula. But its ossification radiates, as in the simple rib-like ilium of the menopome, from a common centre: there are no corresponding multiplications of hæmapophyses below; these are restricted in the pelvis of all animals to the number which they present in the crocodile. And since the scapula has been proved to be, under its most expanded form, the homologue of a single pleurapophysis, so also its homotype, the ilium, must be regarded as maintaining, under every variety of form and proportion, the same fundamental singleness of character which it presents on its first appearance in the perennibranchiate batrachian.

The rudimental hind-limb in serpents is suspended in the flesh and attached only indirectly by one of its simple muscles to the bifurcate and shortened rib of the anterior caudal vertebra: that pleurapophysis, therefore, is but little more modified than the one which represents the ilium in the proteus, and the diverging appendage is as simple as in the lepidosiren, consisting of fewer joints, even where best developed as in the boa, and being reduced to a single osseous style in the slow-worm.

In the air-breathing Vertebrata the typical character of the pelvic arch is progressively disguised by excess of development as we ascend from the low point at which we commenced its analysis; and, in descending below the same low point to the water-breathing class, we find the pelvic arch deviating from its typical character by defective development. And for this indeed we might have been

prepared by the consideration of the close relation which this arch and its appendages bear to locomotion and support of the body on dry land.

In fishes (Pl. I. fig. 2) we find the fin-like homologue of the hind-limbs (v) radiating from a bone (63) which converges to its fellow at the median line, and which is recognised by some anatomists as the 'pubis'; by others, and with better reason, as the 'ischium'; but which is evidently the same abstract vertebral element, viz. a 'hæmapophysis.' The ilium, if it be developed, retains its character as a short, free, or false rib, like 62, its development not proceeding so far as to effect the normal junction with the hæmapophysis. This lower element therefore of the arch being liberated from its typical connections, has no fixed position in the class of Fishes, but in some existing species and all the primæval forms of fishes, keeps near its proper segment, as at v, fig. 2. Pl. I.; and that this is its true position in relation to the archetype, is significantly indicated by the fact that all the fishes in the geological formations anterior to the chalk are 'abdominal.' In certain species of the actual creation the ventral fins advance to the place marked v′ in fig. 2, the ischium elongating to join the coracoid, just as one detached costal cartilage is suspended from another at the back of the thorax in certain birds. By the shortening of the attached ischium, the ventral fins, in other existing fishes, are brought forwards to v″.

In Pl. I. fig. 9, the elementary condition of the hind-limbs in the vertebrata is shown in nature in a back view of the pelvic vertebra of the *Protopterus* or lepidosiren. The letters signify the general and the figures the special homologies of the parts. The apical elements (hæmapophyses or ischia, 63) of the inverted arch are detached from the basal ones (pleurapophyses or 'ilia,' 62) and from the rest of their segment, and carry with them the diverging appendages (65–69), as in all other fishes.

The true meaning and nature of this piscine condition

is beautifully illustrated if we now return, by one step in advance, to the point from which we commenced the analysis of the pelvic arch and limbs.

In fig. 10. Pl. I. *e. g.* the hæmal arch retains its natural connections with the rest of its vertebra, and henceforth preserves them, with a few exceptions (*Enaliosauria* and *Cetacea*), in all the air-breathing classes, up to and including man.

In respect of the modification by displacement, the numerical examples of adhesion to and of departure from type are reversed in the pelvic segment, as compared with the occipital one. Mammals, birds and reptiles show the rule of connection, and fishes the exception, typically as well as numerically. There has been, therefore, no difficulty or discrepancy of opinion in regard to the homology of the detached hæmal arch and its appendages in fishes. Cuvier saw in 63, fig. 2, the representative of the 'os innominatum' or 'os du bassin;' and, notwithstanding the degree of displacement to which such rudiment of a pelvis, with its pelvic members, were subject in fishes, Linnæus had as little hesitation in recognizing in the ventral fins the homologues of hind-limbs wherever they were placed. When in their normal position, as at v, fig. 2, they characterized the 'abdominal' fishes; when advanced to beneath the pectoral fins, as at v′, they characterized the 'thoracic' fishes; when still more advanced, as at v″, they characterized the 'jugular' fishes. The species in which the ventral fins were absent were 'apodal,' in the philosophic language of the immortal Swede. He knew them to be hind-feet under their webbed disguise.

Now all that is here required, in regard to the determination of the locomotive members, is, that no more value be given to the character of detachment and change of place in regard to the scapular arch and its appendages than Linnæus allowed in the case of the pelvic arch and its appendages.

The arms are shifted to and fro in the bodies of the air-breathing vertebrates, the legs in those of the water-breathing vertebrates: the arch supporting the arms is fixed in its true place in fishes, and the arch supporting the legs retains its true place in the higher classes; only it is often necessary that it should be so developed as to be applied to many segments besides the one to which it properly belongs. In the proteus (fig. 10), however, the ilium (62) retains its simple primitive rib-like form, just as the scapula (51) does in fig. 8; and it is connected, as we saw likewise in the menopome (p. 74, fig. 11), to its own vertebra exclusively.

Wherever either arch with its appendages may be situated, it is in its best possible place in relation to the exigences and sphere of life of the species. It is only when we consider its relations to the ideal exemplar that we are compelled to use the terms expressive of rule and deviation.

When a truth is arrived at, the conception of it is clear, and it can be expressed plainly and intelligibly. When the inquirer stops short of, or goes astray from, his aim, yet thinks he has gained it, he can only have a distant and cloudy notion of it, and his definitions must partake of the obscurity of his conceptions. When Oken, after recognising in the scapula an aggregate of cervical ribs, afterwards defined the limbs as 'liberated ribs,' we perceive that neither his notion of ribs, or of the scapular arch, or of limbs, could be clear. When Carus explains the nature of limbs by calling them 'tertiary vertebræ,' we discern the same obscurity in his idea of the primary segments of the skeleton.

According to my definition of a vertebra, we recognise in it the centrum, the neural arch, the hæmal arch, and the appendages diverging or radiating from the hæmal arch. The centrum, though the basis, is not less a part of a vertebra than are the neurapophyses, hæmapophyses; pleur-

apophyses, &c.; and each of these parts is a different part from the other: to call all these parts 'vertebræ' is in effect to deny their differential and subordinate characters, and to voluntarily abdicate the power of appreciating and expressing them. The terms 'secondary' or 'tertiary vertebræ' cannot, therefore, be correctly applied to the parts or appendages of that natural segment of the endoskeleton to the whole of which segment the term 'vertebra' ought to be restricted.

So likewise the term 'rib' may be given to each moiety of the hæmal arch of a vertebra; although I would confine such special appellation to the pleurapophyses when they present that long and slender form characteristic of the thoracic abdominal region, viz. that part of such modified hæmal or costal arch to which the term 'vertebral rib' is applied in anatomy and the term 'pars ossea costæ' in anthropotomy: but, admitting the wider application of the term 'rib' to the whole hæmal arch under every modification, yet the bony diverging and backward projecting appendage of such rib or arch is something different from the part supporting it.

ARMS AND LEGS, therefore, ARE DEVELOPMENTS OF COSTAL APPENDAGES. They are not ribs that have become free: although liberated ribs may perform analogous functions, as in the serpents and the *Draco volans*.

Having thus attained the end proposed as the subject of the present discourse, let us finally apply the few minutes that remain of the allotted time to the contemplation of the abstract Archetype skeleton, as illustrated in fig. 1, Pl. I.

The pectoral and ventral limbs are there exhibited as the appendages of the fourth and twenty-sixth segments: the occipital segment is always the fourth, the pelvic segment has no fixed place or numerical symbol. The lepidosiren realizes, very closely, the primitive condition of the limbs, as exemplified in the ideal archetype.

We have been accustomed to regard the vertebrate animals as being characterized by the limitation of their limbs to two pairs, and it is true that no more diverging appendages are developed for station, locomotion and manipulation. But the rudiments of many more pairs are present in many species. And though they may never be developed as such in this planet, it is quite conceivable that certain of them may be so developed, if the Vertebrate type should be that on which any of the inhabitants of other planets of our system are organized.

The conceivable modifications of the vertebrate archetype are very far from being exhausted by any of the forms that now inhabit the earth, or that are known to have existed here at any period.

The naturalist and anatomist, in digesting the knowledge which the astronomer has been able to furnish regarding the planets and the mechanism of the satellites for illuminating the night-season of the distant orbs that revolve round our common sun, can hardly avoid speculating on the organic mechanism that may exist to profit by such sources of light, and which must exist, if the only conceivable purpose of those beneficent arrangements is to be fulfilled. But the laws of light, as of gravitation, being the same in Jupiter as here, the eyes of such creatures as may disport in the soft reflected beams of its moons will probably be organized on the same dioptric principles as those of the animals of a like grade of organization on this earth. And the inference as to the possibility of the vertebrate type being the basis of the organization of some of the inhabitants of other planets will not appear so hazardous, when it is remembered that the orbits or protective cavities of the eyes of the Vertebrata of this planet are constructed of modified vertebræ. Our thoughts are free to soar as far as any legitimate analogy may seem to guide them rightly in the boundless ocean of unknown truth. And if censure be merited for here indulging, even for a moment, in pure

speculation, it may, perhaps, be disarmed by the reflection that the discovery of the vertebrate archetype could not fail to suggest to the Anatomist many possible modifications of it beyond those that we know to have been realized in this little orb of ours.

The inspired Writer, the Poet and the Artist alone have been privileged to depict such.

Something also I would fain add with a view to remove or allay the scruples of those who may feel offended at any expressions that seem to imply that any part or particle of a created being could be made in vain.

Those physiologists who admit no other principle to have governed the construction of living beings than the exclusive and absolute adaptation of every part to its function, are apt to object to such remarks as have been offered regarding the composition of the skeleton of the whale's fin and of the chick's head, that 'nothing is made in vain;' and they deem that adage a sufficient refutation of the idea that so many apparently superfluous bones and joints should exist in their particular order and collocation in subordination to another principle; conceiving, quite gratuitously in my opinion, the idea of conformity to type to be opposed to the idea of design.

But let us consider the meaning which in such discussions is commonly attached to the phrase 'made in vain.' Were the teleologist to analyse his belief in the principle governing organization, he would, perhaps, find it to mean, that so far as he can conceive of mechanism directly adapted to a special end, he deems every organic mechanism to have been so conceived and adapted. In a majority of instances he finds the adaptation of the organ to its function square with his notions of the perfection of a machine constructed for such an end; and in the exceptional cases, where the relation of the ascertained structure of an organ is not so to be understood, he is disposed to believe that that structure may

be, nevertheless, as directly needed to perform the function, although he perceives that function to be a simple mechanical action, and might conceive a more simple mechanism for performing it. The fallacy perhaps lies in judging of created organs by the analogy of made machines; but it is certain that in the instances where that analogy fails to explain the structure of an organ, such structure does not exist 'in vain' if its truer comprehension lead rational and responsible beings to a better conception of their own origin and Creator*. Our philosophic poet felt that—

> "'Tis the sublime of Man,
> Our noontide majesty, to know ourselves
> Parts and proportions of a wondrous whole."—*Coleridge.*

Nor could the ignorance of this truth be without its benumbing and bewildering influence on the human mind.

The learned Cudworth tells us that—"The Democritick Atheists reason thus: If the World were made by any Antecedent Mind or Understanding, that is, by a Deity; then there must needs be an 'Idæa' and 'Exemplar' of the whole world before it was made, and consequently actual knowledge, both in order of Time and Nature, before Things."

But these Democritans arguing of knowledge as it is got by our finite minds, and ignorant of any evidence of an ideal Archetype for the world or any part of it, concluded that there could be no knowledge or mind before the world, as its cause. And in the same spirit Lucretius asks:

> "Exemplum porro gignundis rebus et ipsa
> Notities hominum Divis unde insita primùm,
> Quid vellent facere ut scirent animoque viderent?"

Now, however, the recognition of an ideal Exemplar for the Vertebrated animals proves that the knowledge of such

* "L'ensemble de tous les ordres de perfections relatives, compose la perfection absolue de ce tout. L'Unité du dessein nous conduit à l'unité de l'intelligence qui l'a conçu."—*Bonnet, Contemplations de la Nature.*

a being as Man must have existed before Man appeared. For the Divine mind which planned the Archetype also foreknew all its modifications.

The Archetypal idea was manifested in the flesh, under divers such modifications, upon this planet, long prior to the existence of those animal species that actually exemplify it.

To what natural laws or secondary causes the orderly succession and progression of such organic phænomena may have been committed we as yet are ignorant. But if, without derogation of the Divine power, we may conceive the existence of such ministers, and personify them by the term 'Nature,' we learn from the past history of our globe that she has advanced with slow and stately steps, guided by the archetypal light, amidst the wreck of worlds, from the first embodiment of the Vertebrate idea under its old Ichthyic vestment, until it became arrayed in the glorious garb of the Human form.

DESCRIPTION OF PLATE I.*

This Plate includes diagrams of the ideal pattern or archetype of the vertebrate endoskeleton, and of the modifications of it characteristic of the four great divisions of the vertebrate subkingdom, viz. fishes, reptiles, birds, and mammals, and also of man.

In each figure the parts or 'elements' of the four anterior segments—the seat of the chief modifications in relation to the lodgement of the brain, the action of the jaws and tongue, and the interposition of the sense-organs—are numbered as in the column of *Nomina* in the Plate.

As the four anterior segments of the neural axis are called collectively 'brain' (*encephalon*), so the four corresponding segments of the vertebral axis are called collectively 'skull' (*cranium*). The head therefore is not otherwise a repetition of the rest of the body, than insofar as each segment of the skull is a repetition or 'homotype' of every other segment of the body; each being subject to modifications which give it its individual character, without obliterating its typical features. So neither are the 'arms' and 'legs' repeated in the head in any other sense than as the cranial segments may retain their diverging appendages. The 'fore-limbs' are actually such appendages of the occipital vertebra, which undergo modifications closely analogous to those of the appendages of the pelvic segment or 'hind-limbs.' And inasmuch as in one class the pelvic appendages, with their supporting hæmal arch, are detached from the rest of their segments, and subject to changes of position (fig. 2, V, V′, V″), so also in other classes the appendages of the occipital segment are liable to be detached with their sustaining hæmal arch, and to be transported to various distances from their proper centrum and neural arch.

* The Plate and the description are taken from my work 'On the Archetype and Homologies of the Vertebrate Skeleton,' 8vo, Van Voorst, 1848.

The head therefore is not a virtual equivalent of the trunk, but is only a portion, *i. e.* certain modified segments, of the whole body.

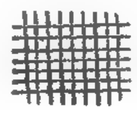
The jaws are the modified hæmal arches of the first two segments; they are not 'limbs' of the head*.

The different elements of the primary segments are distinguished by peculiar markings:—

the neurapophyses by diagonal lines, thus:— 

the diapophyses by vertical lines:— 

the parapophyses by horizontal lines:— 

the *centrum* by decussating horizontal and vertical lines:— 

the pleurapophyses by diagonal lines:— 

the hæmapophyses by dots:— 

the appendages by interrupted lines:— 

the neural spines and hæmal spines are left blank.

In certain segments the elements are also specified by the initials of their names, as in the third segment in fig. 1, and the fourth in fig. 2, for example:—

ns is the neural spine.
n is the neurapophysis.
pl is the pleurapophysis.
c is the centrum.
h is the hæmapophysis.
hs is the hæmal spine.
a is the appendage.

Fig. 1. Ideal pattern or archetype of the vertebrate endoskeleton, as shown in a side-view of the series of typical segments, osteocommata, or 'vertebræ' of which it is composed, the ex-

* These are counter-propositions to Oken's "Der Kopf ist der ganze Rumpf mit allen seinen Systemen," &c., 'Lehrbuch der Natur-philosophie,' 8vo, p. 300, 1843. See the Translation of this Work published by the Ray Society. "The head is the whole trunk with all its systems, the brain is the spinal marrow, the skull the vertebral column, the mouth intestine and abdomen, the nose lung and thorax, the jaws are members or limbs."—P. 364, Prop. 2072.

treme ones indicating the commencement of those modifications, which, according to their kind and extent, impress class-characters upon the type.

The four anterior neurapophyses, 14, 10, 6, 2, give issue to the nerves, the terminal modifications of which constitute the organs of special sense.

The first or foremost of these is the organ of smell (18, 19), always situated immediately in advance of its proper segment, which becomes variously and extensively modified to inclose and protect it.

The second is the organ of sight (17), lodged in a cavity or 'orbit' between its own and the nasal segment, but here drawn above that interspace.

The third is the organ of taste, the nerve of which (gustatory portion of the trigeminal) perforates the neurapophysis (6) of its proper segment (*vertebra parietalis* seu *gustatoria*), or passes by a notch between this and the frontal vertebra, to expand in the organ which is always lodged below in the cavity called 'mouth,' and is supported by the hæmal spine (41, 42) of its own vertebra.

The fourth is the organ of hearing (16), indicated above the interspace between the neurapophysis of its own (occipital) and that of the antecedent (parietal) vertebra, in which interspace it is always lodged; the surrounding vertebral elements being modified to form the cavity for its reception, called 'otocrane.'

The mouth opens at the interspace between the hæmal arches of the anterior and second segment; the position of the vent varies (in fishes), but always opens behind the pelvic arch (Pv) when this is ossified.

Outlines of the chief developments of the dermoskeleton, in different vertebrates, which are usually more or less ossified, are added to the endoskeletal archetype; as, *e. g.* the median horn supported by the nasal spine (15) in the rhinoceros; the pair of lateral horns developed from the frontal spine (11) in most ruminants; the median folds (DI, DII) above the neural spines, one or more in number, constituting the 'dorsal' fin or fins in fishes and cetaceans, and the dorsal hump or humps in the buffaloes and camels; similar folds are sometimes developed at the end of the tail, forming a 'caudal' fin, C, and beneath the hæmal spines, constituting the 'anal' fin or fins, A, of fishes, or the subcaudal dermo-adipose tumour of the Cape-sheep.

Fig. 2. Typical skeleton of a fish (class *Pisces*). The plane of

the anterior hæmal arch (20, 21, 22) is here raised to parallel with the axis of the trunk, and its apex or spine (22) is modified and developed so as to articulate with the neural spine (15) of the same segment, which thus becomes closed anteriorly; both 22 and the hæmapophysis 21 are developed downwards and backwards in relation to the protractile and retractile motions of the arch; and, for the purpose of associating these motions with corresponding ones of the succeeding hæmal arch, the diverging appendage is subdivided (23 and 24) and developed so as to articulate with the pleurapophysis (28) of the next arch; a rudiment of an appendage (26) is attached in some fishes to the hæmapophysis (21) of the nasal segment, but it will be observed that no new element is added to the hæmal arch; and, although the *Lepidosteus* offers an exceptional instance of subdivision of the pleurapophysis (21), that kind of modification is usually restricted to the diverging appendage.

In the next segment the hæmal arch has been the seat of unusual growth, but retains more of its normal position and attachments. Its weight and that of the appendages it supports have required an extension of the proximal articulation of its pleurapophysis (28 *a*) from its proper parapophysis (12) backwards to the next parapophysis (8); and the pleurapophysis itself is subdivided into two, three, or four overlapping pieces for the final purpose explained in my Work "On the Archetype," &c. p. 112; but it is evident that no new element has been introduced, because the extremities of the subdivided pleurapophysis (28 *a* and 28 *d*) retain their normal connections, the one with the parapophysis (12), the other with the hæmapophysis (29, 30). This element is also subdivided, for the same final purpose as the pleurapophysis; and its squamous union with the hæmal spine (32) is retained. Yet the connections of 29 with the condyle of the pleurapophysis and of 32 with its fellow, forming the free apex of the inverted arch of the second segment, show that the complexity is the result of adaptive subdivision, and that no new part has been added to the typical elements as exhibited in the archetype (fig. 1, 29–32); every anatomist has recognised the bones so numbered in the fish as the homologue of the single (undivided or anchylosed) bone forming the lower jaw (29–32) of the mammal (fig. 5) and of man (fig. 6). In addition, therefore, to change of shape and proportion, the parts of the archetype may be modified by division and subdivision. And in this respect the pleurapophyses (28) and hæmapophyses (29, 30, 31) of the fish deviate further from the

archetype than the same parts do in the warm-blooded vertebrates. Herein is manifested the early divergence to a special form for the lowest class, which the higher classes do not assume in passing towards their own types. The diverging appendages are the seat of such excess of subdivision with special development of the divided parts, as best to countenance the idea of a superaddition of new parts to the typical element; yet the most essential character of the diverging appendage is retained under its extremest modification, as where it forms the wing of the bird or the arm of man; viz. its connection by one extremity to a hæmal arch, and the free projection of the opposite subdivided extremity, carrying out with it a fold of integument. With regard to the diverging appendage of the hæmal arch of the second segment, its modifications are arrested at different stages of departure from the simple archetypal form (34–37, fig. 1), as explained at pp. 66 and 112 of my Work "On the Archetype," &c. The most common modification in bony fishes is that shown in fig. 2, where it is divided into two segments, and the second segment into three pieces (35, 36, 37), usually broad and flat, for the office explained at p. 112 of the same Work.

The parietal segment, or third counting backwards, has the hæmal arch (38–41) detached from its proper supporting parapophysis (8) by the backward development of 28 *a* of the preceding segment. This is the first example of another modification, viz. that of dislocation, sometimes accompanied by great change of place, which has tended most to obscure the essential nature of parts, and their true relations to the archetype. The principle of subdivision still manifests itself in the elements of the hæmal arch, especially in its spine, 41–43; and in a greater degree by a vegetative repetition of the 'appendage' (44), without departure from its primitive ray-like form.

The pleurapophysis of the occipital segment (50, 51) is divided into two, and its proximal end is usually bifurcate in fishes, articulating like the normal ribs of higher animals, by a 'head' and a 'tubercle' to two points of the neural arch of its segment.

Almost every stage of development and departure from the primitive type is manifested by the diverging appendage (54–57) up to the extent of modification attained by the typical osseous fish. The proximal segment is divided into two pieces (54 and 55), the next segment into four or more (56), and the last segment into

a greater but variable number of pieces, retaining the elementary form of rays.

The Lepidosiren (fig. 7) is eminently instructive by the retention in the occipital vertebra of the primitive condition of the appendage, as shown in the archetype (fig. 1, 53–57) modified only by segmentation of the ray. The pleurapophysis of the arch (51) likewise retains its simple cylindrical form, and is articulated to its centrum, like the other ribs of the Lepidosiren, by an undivided head.

The hæmal arch of the fifth segment (first of the trunk) is commonly detached from its centrum and neural arch in fishes without being displaced backwards. The pleurapophysis (*pl*) is short and simple, sometimes expanded; the hæmapophysis (58, *h*) is simple, long and slender. When this arch supports an appendage it is a simple diverging ray.

All the succeeding abdominal segments of the fish have their hæmal arches incomplete by bone; the hæmapophyses and spines retaining the primitive fibrous condition. The pleurapophyses of most support diverging appendages in the form of simple undivided bony rays.

A part of the hæmal arch of a post-abdominal (pelvic) segment is ossified (63), and supports a more complex appendage (69) in the form of one, two or more jointed rays, which project beyond the surface and are enveloped by a fold of skin forming the 'ventral' fin, V, making a pair with the one on the opposite side. This partially ossified hæmapophysis articulates with its fellow by its anterior apex, forming a 'symphysis ischii' seu 'pubis'; and, in some fishes called 'abdominal,' it is connected to its proper pleurapophysis (62) by an aponeurosis representing its unossified continuation.

The remarkable degree to which one and the same part may be subject to the modification of change of position, is strikingly exemplified in this lower portion of the pelvic arch with its appendages in fishes. It may be moved forwards, so that the symphysis of the pelvic arch is brought into connection with that of the scapular arch; when, according to the length of the ossified parts of the pelvic hæmapophyses, the species is either 'thoracic,' as when the ventral fins are at V′, or 'jugular,' when they are advanced to V″. The universally acknowledged and long recognised special homology of the hæmal arch and appendages of the

pelvic vertebra, as the 'ventral fins' of fishes, under these changes of position, prepare us for the recognition of an analogous modification of the hæmal arch and appendages of the occipital vertebra in the higher classes of Vertebrata.

Beyond the abdomen the osseous and aponeurotic parts of the hæmal arches rapidly contract; the progressively elongated parapophyses usually bend down and complete the inverted arch by their apical coalescence; sometimes distinct pleurapophyses continue to form these arches; sometimes these elements may be traced, anchylosed with their fellows of the opposite side, and with the coalesced extremities of the parapophyses. The bodies of a certain number of the terminal segments coalesce together in the typical osseous fishes, and support several neural and hæmal arches and spines, usually more or less expanded, and forming the basis of the caudal fin, C.

The ossified parts of the dermal median and symmetrical folds, constituting the dorsal (D I, D II), the anal (A), and caudal (C) fins, are added to the endoskeleton in fig. 2; *in* are the interneural spines; *dn* the dermoneural spines; *ih* the interhæmal spines; *dh* the dermohæmal spines; these form no part of the true vertebral skeleton, and are peculiar to fishes. The diagram of the modified cranial segments is not complicated by the outlines of the sense-capsules or mucodermal bones.

Thus, compared with the archetypal figure, the endoskeleton of the fish deviates by excess of development, manifested chiefly in the diverging appendages of the four anterior or cranial segments, and by arrest of development in most of the other segments; but the principle of polaric or vegetative repetition greatly prevails, and more of the segments resemble one another than in any of the higher classes.

Fig. 3. The Crocodile is here taken as the type of the class *Reptilia*.

The hæmal arch of the anterior segment is now firmly fixed by excessive development, chiefly of its hæmapophyses (21), which have extended their attachments to all the elongated elements (13, 14 and 15) of their own neural arch. The diverging appendage (24) from the pleurapophysis (20) fixes the arch extensively to the centrums of the second and third segments: the appendage from the hæmapophysis (21) bifurcates; one branch, divided into two

pieces (26 and 27), connects the arch with the pleurapophysis (28) of the next segment; the other branch (25) extends the attachment to the parapophysis (12) of the same segment, and also to the appendage (24) of its own arch.

The pleurapophysis (28) of the frontal segment is undivided; it is represented as displaced and depressed; but in nature it still retains a small part of its connection with its proper pleurapophysis (12), although it is developed backwards so as chiefly to articulate with that (8) of the following segment: it supports no diverging appendage. The hæmapophysis (29–31) is more subdivided than in fishes, in relation to functions explained in my Work "On the Archetype," &c., pp. 122, 123.

The excess of development of the hæmal arch of the frontal vertebra is compensated by the defect of development of that of the parietal one (40, 41); and this constitutes the next great additional step in the deviation from the archetype. Only the hæmapophyses (40) are ossified: the hæmal spine, though much expanded and flattened, remains cartilaginous, and the pleurapophysis is represented by a feeble ligament. The whole arch is detached and displaced backwards, and its diverging appendages cease to be developed.

The tendency to retrogradation manifested by the preceding hæmal arches is carried out to a striking extent in that (51, 52) of the occipital segment (the fourth counting backwards): it overlaps the homotypal arches of the 8th to the 11th segments of the trunk: the ossified portions of both its constituent elements, 51 and 52, are simple; the hæmal spine, 52′, is prolonged backwards. The diverging appendage manifests, in comparison with that in the fish, an additional segment (53), which is single; the segment of two pieces (54 and 55) is now the second. The rays of the distal segment are reduced to five in number, which is never afterwards exceeded in the vertebrate subkingdom. The dislocation and retrogradation of the posterior hæmal segment of the skull form the second chief additional feature of departure from the archetype, as compared with the skeleton of fishes. The third well-marked modification is the development of an inferior (cortical) portion of the body of the atlas (*ca*, *x*), distinct from the main part of that centrum (*ca*), which coalesces with that of the axis, and is commonly called its 'odontoid' process.

The nine segments that succeed the head resemble those of

fishes in the non-ossification of the hæmapophyses and hæmal spines, but deviate further from the archetype by the minor development of the pleurapophyses. These progressively elongate to the 12th vertebra, where the hæmal arch is completed by a hæmapophysis and hæmal spines.

The hæmapophyses are not so completely ossified as the pleurapophyses, and they are divided from these by the interposition of cartilaginous pieces, *a*, *a*; these pieces may be regarded either as dismemberments of the hæmapophyses, or as unossified parts of the pleurapophyses. The diverging appendages (*a*, *a*) are usually cartilaginous.

Beyond the 21st segment of the trunk* the pleurapophyses usually cease to be represented either by bone or cartilage: but the partially ossified hæmapophyses are continued to those of the pelvic segments, 64 and 63, *h*. In these segments the pleurapophyses reappear, and are divided into two parts, like those in the thorax: the proximal portions (*pl*, *pl*) are short and thick; the distal portions have either coalesced into one broad and thick plate (62 *pl*), or the distal portion of one pleurapophysis is still more remarkably developed and takes the place of two: this question is discussed at pp. 75 and 76. The two hæmapophyses (63, 64) are distinct and well-ossified. The diverging appendage (65–69) has been subject to the same kind and amount of development as that of the scapular arch (53–57). The first steps in the

* According to Cuvier, the pleurapophyses cease to appear after the 20th trunk-vertebra in *Crocodilus biporcatus*, and after the 19th in *Alligator lucius*. I allude to these differences for the purpose of remarking that the conformity of organization is greater than would appear at first sight from the formulæ of the vertebræ of the different species of crocodile cited in the Table at p. 220, tome i. Leçons d'Anatomie Comparée, 1835. The number of vertebræ from the atlas inclusive to the sacrum is the same in each species, as will be seen by the following extract:—

	Cervical.	Dorsal.	Lumbar.		
Crocodile à deux arêtes	7	13	4	=	24
Crocodile du Gange	7	14	3	=	24
Caiman à mus. de brochet	7	12	5	=	24

The difference in the dorsal and lumbar series depends merely on the ossification or otherwise of the pleurapophysial tendons or fibrous bases attached to the diapophyses of the 20th, 21st and 22nd vertebræ.

A slight change in the form and size of the pleurapophysis is all that distinguishes the first dorsal from the last cervical vertebra in the Cuvierian Table.

progression of this metamorphosis from the primitive type is shown in the *Lepidosiren* (fig. 9), and the *Proteus* (fig. 10). The modification of the pelvic segments and their appendages in the reptile forms another prominent feature of deviation from the archetype. The pleurapophyses are continued, progressively shortening, attached to the diapophyses of a certain number of the vertebræ that succeed the sacrum: the hæmapophyses are no longer attached to their extremities, but are directly articulated to the central elements, with a slight degree of displacement, whereby they articulate to another segment as well as to their own. The mode and degree of departure from the archetype are now such that different series of vertebral segments may be classed into groups, with distinctive characters and names :—

The first four segments, by the fixed union of their neural arches, as *cranial* (Cr), under the collective name of 'skull.'

The next nine segments, moveably articulated, and with free or 'floating' pleurapophyses, as *cervical*, C, forming collectively the region called 'neck.'

The succeeding nine segments with ossified and moveable pleurapophyses and hæmapophyses, as *dorsal*, D, forming the 'back,' 'thorax' or 'chest.'

The three following moveable vertebræ, without free bony pleurapophyses, as *lumbar*, L, forming the 'loins.'

The next two vertebræ, immoveably united, and with modified and much-developed hæmal arches and appendages, are called *sacral*, and collectively 'pelvis and hind-limbs.'

All the other segments are '*caudal*' and constitute the 'tail.'

The hæmal arch (51, 52) with the developed appendages (53–57*a*) detached from the occipital vertebra, may require to be specially noticed in this summary of the parts of the endoskeleton, as from the circumstance of its commonly remote position from its proper segment, it may not have been thought of as a part included in the first class of vertebræ constituting the skull.

Many striking and extreme deviations from the archetype are manifested in the skeleton of the more aberrant forms of the reptilia. The number of moveable trunk-segments is reduced to the minimum in the *Batrachia* (*e.g.* 7 in *Pipa*), and increased to the maximum in the *Ophidia* (422 in *Python*). At first view the principle of vegetative repetition seems to have exhausted itself in the long succession of incomplete vertebræ which support the

trunk of the great constrictors: but by the endless combinations and adjustments of the inflections of their long spine, the absence of locomotive extremities is so compensated that the degraded and mutilated serpent can overreach and overcome animals of far higher organization than itself: it can outswim the fish, outrun the rat, outclimb the monkey, and outwrestle the tiger; crushing the carcase of the great carnivore in the embrace of its redoubled coils, and proving the simple vertebral column to be more effectual in the struggle than the most strongly developed fore-limbs with all their exquisite rotatory mechanism for the effective and varied application of the heavy and formidably-armed paws. And whilst the vertebral column of the ophidian order exhibits the extreme of flexibility, that of the chelonia manifests the opposite extreme of rigidity: back, loins and pelvis constitute one vast sacrum, or rather abdominal skull, but a skull subordinated chiefly to the lodgement and defence of a much-developed hæmal system, and in which the pleurapophyses, hæmapophyses and their spines appear to repeat the same modification of great expansion and fixed union by marginal sutures, which the neurapophyses and spines undergo in the cranium of the higher vertebrates. This formation of the 'carapace' is actually due, however, to the connation of dermal bones with the above-named vertebral elements, but in which it is worthy of note that the neurapophyses exhibit the modification of change of position, like that which has been described in the sacrum of the bird; being shifted from their own centrum over one half of the next centrum, thus adding to the strength and elasticity of the whole osseous vault. The plastron is formed by the connation of dermal plates with the sternum and abdominal ribs. The confluence of the neurapophysis (14) with its own moiety of the neural spine (15) is characteristic of the anterior segment of the cephalic skull of most Chelonia. I may here add, that the typical condition of the hæmal (maxillary) arch of the same segment is well shown in the *Emys expansa*. The pleurapophyses (palatines) meet at the base of the cartilaginous vomer, above and behind the posterior nares, sweep outwards and downwards, give attachment to the hæmapophyses (maxillaries) which advance and converge, and the arch is closed below the nasal passage by the hæmal spine (premaxillary). Cut through the junction of the hæmapophyses with the neurapophyses (prefrontals), and with the diverging ap-

pendages (malars), and the inverted arch is then suspended by its proper piers, the pleurapophyses or palatines.

In the connation or coalescence of the neurapophyses and spines forming the parietal and frontal neural arches in the ophidian and some chelonian reptiles, we perceive a return to the common constitution of those arches in the vertebræ of the trunk, in which the permanent separation of the neural spine from the neurapophyses occurs as a rare exception.

In the class-skeleton (*Aves*) represented in fig. 4, the archetype is further departed from than in the typical Reptilia; and when the general form of this diagram is contrasted with that of the first figure, the power of demonstrating the fundamental agreement which reigns throughout, and which is equally manifested in the comparison of figure 4 with those of the piscine and reptilian skeletons, affords a most striking proof of the unity of plan which pervades the whole series.

As compared with the crocodile (fig. 3), the proportions of the hæmapophysis (21) and spine (22) of the anterior segment are reversed; there is a return towards the condition of the parts in fishes (fig. 2); the strength of the arch being chiefly due to the great development and extensive connections of 22, which usually sends a process upwards and backwards between the divided neural spine (15) of its own to that (11) of the next segment. The pleurapophysis (20) has often a slender rib-like form, and the appendages retain the form of bony rays. That (24) from the pleurapophysis is simple; that (26, 27) from the hæmapophysis is divided in the embryo-bird: both concur in attaching the hæmal arch of the anterior segment to the pleurapophysis of the second segment. The neurapophyses of the anterior segment coalesce and form a single vertical bone, slightly expanded above and sometimes appearing anterior to the frontal.

The inferior or cortical part of the centrum, 9, of the second or frontal vertebra is connate, as in the fish (fig. 2, 9), with that of the third, 5; and the superior dismemberment of the second centrum, answering to 9′ in fig. 2, is connate with the coalesced neurapophyses, 10.

The hæmal arch of the second segment is detached from its neural arch; and, although its proper parapophysis (12) some-

times joins the next one (8), yet this exclusively supports, in birds, the pleurapophysis (28) of the frontal segment. The hæmapophysis is developed, as in the reptile, from several centres (29, 29′, 30′, 31), but these coalesce with each other and with the hæmal spine, 32, to form the single bone called lower jaw in most birds.

The hæmal arch (40–46) properly appertaining to 8—the parapophysis of the parietal segment—is detached from it, and freely suspended, somewhat retrograded in position beneath the next segment: its development has suffered as marked an arrest as in the crocodile.

The hæmal arch, with its appendages of the hindmost segment of the skull, is displaced backwards to a greater extent than in the reptile*.

The pleurapophysis (51) retains the form of a long, flat, slightly-arched rib: the hæmapophysis (52) is straighter and stronger. There are birds (*Apteryx*, e. g., fig. 9, p. 47) in which this arch is arrested at almost as early a stage of growth as is the antecedent (hyoid) arch of the skull. The elements of the neural arches of the skull, 1–15, early anchylose together in most birds, with the exception of the centrum (13) of the foremost segment, which more commonly coalesces with the pleurapophyses (20) of its hæmal arch.

The size of the brain now demands a modification of the neural arches superadded to those which they present in the cold-blooded vertebrates, and occasions a marked difference in the form of the skull: it is important to note how this is obtained. The nature of the modification is well shown in the young of those large birds which are devoid of the powers of flight. No new bone is introduced to increase the cranial walls and give the cavity its due

* The process of retrogradation is associated with the difference of time in the order of development of different segments of the endoskeleton. The typical vertebræ are usually the first to be completed, *e. g.* those of the thorax and head; the intervening ones are later developments, and the head is removed from the chest to an extent corresponding with their number or size. But the hæmal arch of the last cranial vertebra being detached in air-breathing Vertebrates from the rest of its segment, follows the heart, which it was primarily developed to support and protect, and consequently maintains its primitive contiguity with the thorax. The original relation of its hæmapophyses —the coracoids—to the pericardium is most instructively maintained in the Chelonia. In the higher air-breathing animals the proper thoracic hæmal arches take this function, and leave the scapular arch to subserve the offices of its greatly and variously developed appendages.

capacity ; this is gained by excess of growth of common and constant elements ; and those (3, 7, 11) furthest from the centrums are the chief seat of such excess. With regard to the neural spines of the frontal and parietal vertebræ, it is accompanied by a temporary bipartition, the ossification commencing from two lateral centres in each ; but the halves soon coalesce with each other and with their sustaining neurapophyses (2, 6, 10).

In those segments which, from the brevity and free termination of the pleurapophyses, may be called 'cervical,' the elements of the neural arch and also the pleurapophyses early anchylose together in each segment, converting it into the single bone, called in comparative osteology a 'vertebra,' and these vertebræ are remarkable for their great number in most birds ; and consequently the neck is as remarkable for its great length and flexibility. The detached hæmapophyses (58) of one of these vertebræ, (which vertebra, by the analogy of the fish (fig. 2, 58), should be the atlas,) commonly coalesced together at their distal ends forming a bony arch, like a slender edentulous lower jaw, have followed the hæmal arch of the occipital vertebra (51, 55) in its retrograde course, though not quite to the same extent. These mutually anchylosed hæmapophyses (58) forming the bone, called 'furculum' in ornithotomy, are generally the only pair of ossified cervical hæmapophyses. If, however, we define the cervical vertebræ, as in the crocodile, by their mobility and the free termination of their pleurapophyses, we may then recognise in some birds the detached hæmapophyses of the last cervical vertebra attached, as at *h*, to those of the succeeding segment : this structure may be observed in the common goose (*Anser palustris*). The pleurapophyses of the posterior cervical vertebræ are free, and rapidly elongate. The hæmapophyses of the segments with complete hæmal arches are bony, and are commonly defined as 'sternal ribs,' their pleurapophyses being called 'vertebral ribs,' agreeably with the restricted anthropotomical meaning of the term 'vertebra.' These pleurapophyses support bony appendages (*a a*), which serve, like those of the foremost hæmal arch of the skull, to connect their own arch to the next and associate them together in movement*.

* These appendages are not the result, as has been supposed, of a bifurcation of the vertebral rib : they are independent pieces originally in all birds, and retain their individuality in some, *e. g.* apteryx, penguin, with proper muscles for their elevation and depression—potential homotypes of the flexors and extensors of more developed limbs.

After six or seven segments with these typical hæmal arches come others with shorter pleurapophyses terminating freely, not reaching their hæmapophyses, one of which, ossified, is shown in the diagram at *h'*, adhering by its distal end to the preceding hæmapophysis and terminating freely above. These 'floating sternal ribs' are more numerous in the crocodile (fig. 3, *h'*). The hæmal spines of the dorsal segments with complete hæmal arches become the seat of the most extensive and characteristic modifications of the avian type of skeleton. They are greatly extended in breadth, and, like the correspondingly expanded neural spines of the cranial vertebræ, are developed from two lateral moieties; but the individual spines, indicated by dotted lines in the diagram (60), are not ossified from separate centres, but continuously, so that the hæmal spines of six or eight vertebræ are at first represented by a pair of osseous plates. A cartilage is usually extended vertically from their median junction, which, when ossified, forms a strong crest or 'keel' (60'). The hæmal spine of the scapular arch (52') is sometimes ossified from a proper centre; as is also a piece prolonging the series posteriorly: but all soon coalesce into one bone called 'sternum.' The anterior portion, 52', has received the name of 'episternum,' the median keel, 60', that of 'entosternum,' the posterior piece, which sometimes remains cartilaginous, that of 'xiphisternum.' In the terrestrial birds incapable of flight, the keel or 'entosternum' is not developed: in the rest of the class the extent of this part and of the ossified portion of the body of the sternum bears a direct ratio to their power of flight; the peculiar modification of these extreme elements of the dorsal segments being governed by the size of the muscles moving the wings.

The next great deviation from the typical standard, peculiar to birds, is the great extent of the vertebral axis which is embraced by the enormously developed pelvic pleurapophyses, 62, and the unusual number of segments which, being thus deprived of reciprocal motion, grow together and form, according to this character, the bone or region called 'sacrum.' In investigating the structure of this part of the endoskeleton in the embryo-bird, the neural arches are found to manifest a change of position analogous to, though less extensive than, that of certain of the hæmal arches of more anterior segments (51–52, *e. g.*): the results of this analysis are detailed at p. 61. Most of the pleurapophyses of the sacral vertebræ are stunted in their growth, which may

literally be said to be stopped by the pressure upon their extremities of the overgrown distal portion of one of their homotypes, forming the bone called 'ilium' (62, *pl*). But one or two of the pleurapophyses at the anterior part of the series (*pl*) escape from beneath the 'ilium' to terminate freely at some distance below it: these are usually bifurcate at their proximal ends, and moveably articulated to their anchylosed centrums and diapophyses: the shorter anchylosed sacral pleurapophyses have simple proximal ends and articulate in the embryo to the interspace between their own and the adjoining centrum, as shown in fig. 10, *pl*, p. 61, to which they soon become anchylosed.

The contemplation of the modifications of the different natural segments in the trunk of the bird, particularly the freedom of some elements and the fixation of others, strongly impresses on the mind the purely artificial character of the regions of the spine which have been transferred from anthropotomy into the anatomy of the vertebrate animals. Thus Cuvier declares, "Il n'y a point de vertèbres lombaires proprement dites*." And a later author:— "Die Wirbel zerfallen in Hals- Rücken- Kreuzbein- und Stusswirbel; eigentliche Lendenwirbel sind gewöhnlich nicht zu unterscheiden."

Cuvier's negation in 1799 of proper lumbar vertebræ in birds is reproduced in succeeding systems and handbooks of comparative anatomy down to the latest by Siebold and Stannius, *e. g.* of 1846. But the student of anatomy in its wider acceptation will understand that the segments homologous with those included under L in fig. 3 are by no means wanting in fig. 4, but only otherwise modified.

It may be regarded as highly probable at least, from the striking points of agreement which are observable in the organization of the crocodile and of the bird, that, counting backwards from the first 'dorsal' in figs. 3 and 4, the next twenty segments are homologous in both. But, in the bird, those that answer to the three or four last dorsal vertebræ in the crocodile are anchylosed together, and the last of these had its pleurapophyses modified to form abutments against the elongated ilia. The next three segments, answering to the lumbar in the crocodile, are modified as in the last 'dorsal.' The two following segments similarly modi-

* Cuvier, Leçons d'Anatomie Comparée, i. (Ed. 1799, p. 170; Ed. 1836, p. 205).

fied will answer then to the two sacral vertebræ of the crocodile, and anchylosis extends backwards so as to include two or three vertebræ homologous with the anterior caudals in the crocodile. This appears to be the true interpretation of the enormous 'sacrum' of the bird; it is not merely 'lumbo-sacral' but 'dorso-lumbo-sacro-caudal,' including as it does representatives of each of those classes of vertebræ in the crocodile, but which have lost the artificial characters that distinguished them in that nearest allied existing vertebrate. The special homologies are indicated by the letters D, L and S.

The characters of the regions of the vertebrate skeleton are, as already remarked in reference to the crocodile, artificial, and are used for the sake of convenience in describing and comparing the vertebræ of different species. Those, therefore, are the best which are the most constant and most readily applicable in any given class. Proceeding to assign such to the bird, as in the crocodile, unbiased by anthropotomical characters of the vertebral regions, all those may be called 'cervical' in the bird that extend from the skull to the first vertebra with the hæmal arch complete, and those dorsal that extend from that vertebra inclusive, to the first vertebra embraced by, and anchylosed to, the iliac bones. One usually finds in the falcons, the gallinaceous birds and in some waders, five or six of the centrums and neural arches of the dorsal vertebræ anchylosed into one mass, a single free centrum usually intervening between this mass and the true sacrum. Some comparative anatomists call that cervical vertebra the 'first dorsal' in which the pleurapophyses retain, or begin to regain, their moveable articulations: but this character varies in different individuals of the same species. I have even found the pleurapophysis of the last cervical vertebra anchylosed on one side and not on the other.

The retention by the pleurapophyses of moveable articulations with the centrum, might also seem a good character of dorsal vertebræ at the hinder end of the series; but it is inconstant: I have found those elements anchylosed in one individual and free in another of the same species, in the anterior vertebræ, which are sacral by coalescence. All those vertebræ may be called for convenience 'sacral' in the bird, which are confluent by both centrums and neural arches with each other and with the iliac bones; and this confluence is so complete that it usually requires a vertical section and reference to the nerve-outlets in order to determine their

number. The free vertebræ that succeed these are the caudal, of which the last, as in most osseous fishes, is a coalesced congeries of several, though for convenience counted as one, and called in ornithotomy the plough-share bone (*c*, *n*, *h*). Although so many segments of the bird's skeleton are modified to transfer the weight of the horizontal trunk upon the ilia (62), the 'pelvis,' as in the crocodile, has but two hæmapophyses, 63, 64, below: it is characteristic of birds, however, that these are not united at their distal ends to their fellows of the opposite side, either with or without the intervention of a hæmal spine. The exception which the ostrich offers in regard to the anterior pair (pubic bone, 64) and that which the rhea presents in respect to the posterior pair (ischia, 63), serve to prove the rule of the inferiorly open pelvis in birds.

In regard to the diverging appendages of the two hæmal arches (scapular and pelvic) which have been selected for development into locomotive organs in all classes of vertebrata, the corresponding segments (carpal, 56, and tarsal, 68) agree in the paucity of their divisions, two bones in each, in all birds; and the succeeding segments (metacarpal and metatarsal) in consisting of three coalesced bones in both wing and leg, supporting digits answering to those marked II, III and IV, *ii*, *iii*, *iv*, in the crocodile. Such at least is their general character, the minor differences being the following:—In the hand-segment of the wing the anchylosed metacarpal of digit II is very short, represented as it seems only by its proximal end; those of the digits numbered III and IV attain their normal length, and are anchylosed together at the extremities only, with an interspace between their shafts.

The wing of the bird is chiefly formed by the quill-feathers, developments of the hard, insensible epidermal system: and this expanse forms a striking contrast with the delicately organized and highly sensitive web which is stretched over the long and slender finger-bones of the bat. Its period of activity in the hours of gloom necessitated the accessory sense of fine touch in aid of vision to safely guide its flight.

In the metatarsus of the bird the three bones coalesce throughout their length, except in the penguin, where interspaces are left between their shafts or middle parts. But they also coalesce proximally with the two primitively distinct tarsal bones (68), whilst the metacarpals coalesce proximally with only part of the carpal

series, if at all. And to the metatarsus there is usually superadded a rudimental, but unanchylosed, metatarsal bone of the digit answering to no. 1 in the crocodile; but directed backwards, except in the swift. The numbers of the phalanges of the toes, *i*, *ii* and *iii* in birds, correspond with those of their homologues in the crocodile: the toe *iv* has an additional phalanx, and the regular progression of the increase from two to five phalanges, with one or two exceptions, is constant in the class, and serves to determine the toes in those birds in which they are reduced to three or two in number. Thus in the ostrich (fig. 11), the shorter of the two toes is determined by its greater number of phalanges, 5, to be the homologue of the fourth in tetradactyle birds; and it is interesting to observe that the toe *iii*, notwithstanding its much greater length, has the usual smaller number of phalanges. But whilst unity of design is thus manifested, the wisdom of the Designer is displayed by the greater strength which results from the minor degree of subdivision of the part which takes the largest share in the support and propulsion of the body. The toe *v* is never present in birds; there is not even the rudiment of its metatarsal bone. The toe *i* is equally absent. (See paragraph at p. 36, on the spurs of the *Gallinacea*.)

Fig. 4 is the diagram of the skeleton of a typical mammalian quadruped; *e. g.* the dog (genus *Canis*). The modifications of the hæmal arch of the anterior segment resume the characters of those in the crocodile; the hæmapophysis (21) being the chief seat of development, and for the same purpose of extending its attachments, and adding to the firmness and strength of the henceforth immoveable maxillary arch. The diverging appendage from the pleurapophysis (20) is a single bone on each side (24), and in most mammals becomes confluent with the part of the posterior segment (5) against which it abuts.

The neurapophyses (14) of the anterior segment have coalesced together, as in birds, but are complicated and their nature further obscured by anchylosis with ossified portions of the olfactory capsules, often extremely complex and extensive in the class Mammalia, in which the organ of smell attains its maximum of development. The neural spine (15), sometimes single, more frequently bifid, enjoys, agreeably with its extreme position in the series, a vast range of variety in its forms and proportions. In the rhinoceros it supports a dermal spine or 'horn.'

The second (frontal) segment presents unexpectedly a return to the archetypal character in a particular, in the absence of which all the lower classes of vertebrata depart from it, viz. the primitive independence of its centrum (9) from that (5) of the succeeding segment. The spine (11) of this, as well as those (7, 3) of the two following segments, continue, as in birds, to be the chief seat of the expansion requisite for the protection of the progressively developing brain. But in most mammals an additional element in the cranial walls is gained by the expansion of the distal end of the diverging appendage from the hæmopophysis (21) of the anterior segment. This appendage consists, as in birds and reptiles, of two pieces, and it is the second or most remote piece (27) which is the seat of the principal varieties, and especially of that squamous development which enables it not only to extend the points of fixation of the maxillary arch, but at the same time to subserve the requirements of cranial space consequent on the large size of the cerebrum. The dismemberment called 'interparietale,' *x*, of the spine 3, has a less constant relation to the increased capacity of the cranium.

The pleurapophysis (28) of the second segment becomes, in the present class, still further displaced from its typical connections, and is even superseded in its typical functions by the intervention and development of 27. It is consequently much reduced in size, and strangely distorted in form, in subserviency to the almost sole office that now remains to it, viz. the support of the tympanic membrane.

The frontal hæmapophyses and spine (29–32) have coalesced into a single bony arch, articulated by its extremities to the under part of the appendage 27.

The pleurapophysis (38) of the hyoid or third hæmal arch resumes in many mammals its typical connections with the parapophysis (8) of its proper segment; but its development is usually more or less restricted.

The articulation of the fourth (occipital) segment with the succeeding one called 'atlas,' is chiefly by means of zygapophyses (condyles) developed from the neurapophyses (2); the parapophyses (4) are likewise exogenous processes of the same elements.

The hæmal arch of the occiput (51, 52), though in close proximity with its proper neural arch in some mammals, and in all mammals at the earlier period of development, is not directly

articulated thereto, and sometimes recedes far from the rest of the skull.

The hæmapophysis (52) of the arch is ossified throughout its entire extent and articulated with the hæmal spine 52′, below, in only one small exceptional order of the class (*Monotremata*). It becomes anchylosed with the pleurapophysis in all, and appears in the majority therefore as a mere process of 51.

The single pair of cervical hæmapophyses (58) are more variable, both as to their extent of ossification and even existence.

The body of the atlas continues subject to the same modification of development from two centres with coalescence of one portion with the next centrum, which characterises it in all the other vertebrates above Batrachians*.

The confluence of the centrum with the neural arch takes place in every vertebra of the trunk; and the pleurapophyses, which are very short in the seven segments that succeed the skull, here also commonly coalesce with the other elements, circumscribing the lateral foramina for the 'vertebral' arteries. With the exception of the detached bones 58, they are the only ossified parts of the hæmal arches of those segments.

The constancy of the number, *seven*, of the segments so modified, is truly remarkable and characteristic of the class Mammalia. It is true that the number is established at a very early stage of development, when the neck is alike short in all; and its law must be sought for in the circumstances, such as the existence of a complete diaphragm in the mammalia, which determined the number and distribution of the pairs of cervical nerves, upon which the development of the cervical vertebræ more immediately depends. The exceptions to the number *seven*, viz. *six* in the manatee, and *eight* or *nine* in the three-toed sloths, serve to establish the rule.

The eighth segment of the trunk in mammalia, like the tenth in the crocodile, has a complete hæmal arch, and here therefore the 'dorsal' series begins; but the hæmapophysial elements are rarely ossified in the present warm-blooded class.

The pleurapophyses (*pl*) of these arches are not only moveable, but are subject to a slight displacement, and their articulations, like those of the neurapophyses in the bird's sacrum, extend over the interspace of their own and a contiguous centrum.

* See Taylor's Annals and Magazine of Natural History, vol. xx. p. 217.

The hæmal spines (60, 61, *hs*) commonly remain distinct, and form a chain of ossicles corresponding in number with the complete hæmal arches, but they coalesce with each other in some of the higher mammalia, and are called collectively 'sternum.'

As the segments recede the pleurapophyses become shorter, return to their proper vertebra, and usually become appended to its diapophyses; the hæmapophyses also become shorter, and terminate at first by abutting against their antecedents, and finally by projecting freely.

These segments are followed by others (L) in which only the pleurapophysial parts (*pl*) of the hæmal arch are ossified, and these parts coalesce with the diapophyses (*d*).

Then come the segments (S), which, like those of the skull, are the seat of the modification by anchylosis, and of great and peculiar development of two of the hæmal arches in connection with them; the nature of the deviations from the typical standard which characterise the province of the endoskeleton called 'sacrum' and 'pelvis,' has been explained at pp. 61 & 73. In most mammals a greater number of segments is involved in this metamorphosis than in reptiles; in none are so many the seat of it as in birds. In the cetacea the modification by anchylosis is transferred to segments at the fore-part of the trunk; their 'sacrum' may be said to be in the neck; none of the post-abdominal vertebræ are subject to confluence any more than in serpents, fishes, or the extinct marine reptiles (*Enaliosauria*).

Great diversity of form, of number and of development prevails in the vertebræ that succeed the sacrum in mammalia. Short pleurapophyses are developed at the extremities of the diapophyses of the anterior ones and coalesce with them. The hæmapophyses, when present or ossified, are articulated, as in reptiles, to the centrum directly, and alone form the hæmal arch. The terminal vertebræ are reduced to the central element, and rarely anchylose together.

The anterior anchylosed and expanded vertebræ are the cranial, Cr.

Those usually free vertebræ with short pleurapophyses, anchylosed to both their centrum and neural arch, are called 'cervical,' C. In some whales and armadilloes all or some of these vertebræ coalesce into one mass.

The series with moveable and usually longer pleurapophyses is called 'dorsal,' D.

Those with pleurapophyses confluent or connate with the extremities of the diapophyses are called 'lumbar,' L.

The succeeding vertebræ which anchylose together are called 'sacral,' S.

The rest are 'caudal,' Cd.

The modifications of the diverging appendages of the scapular and pelvic arches are numerous in kind and extreme in degree: with the exception of the cetacea, in which the hinder pair is absent—the cheiroptera, in which the fore-pair is specially developed for the actions of flight—and some burrowers, as the mole—a close analogy is commonly kept up between the two pairs: both, for example, are reduced to the same degree of simplicity in the solid-ungulous horse; both arrive at almost the highest stage of development, in the special adaptation of one of the digits to react upon the rest as an opposable thumb in both the fore- and hind-feet of the Quadrumana.

Fig. 15, bones of the fore-limb, and fig. 16, bones of the hind-limb, of the Wombat, illustrate the serial homology of those bones, explained at pp. 23 & 24.

53, 'humerus,' is the homotype of 65, 'femur.'

54, 'ulna,' is the homotype of 67, 'fibula.'

o, 'its olecranon,' is the homotype of 67′, 'fabella,' or the sesamoid bone articulated to the produced and expanded head of the fibula.

55, 'radius,' is the homotype of 66, 'tibia'*.

sc, scaphoid portion of 'os scapholunare,' is the homotype of *sc*, 'scaphoides.'

l, lunar portion of 'os scapholunare,' do. of *a*, 'astragalus.'

cu, cuneiform portion of 'os scapholunare,' do. of *cl*, articular part of 'calcaneum.'

p, 'pisiforme,' is the homotype of *cl′*, fulcral part of 'calcaneum,'

t, 'trapezium' do. of *ci*, inner cuneiform.

z, 'trapezoides' do. of *cm*, middle cuneiform.

m, 'magnum' do. of *ce*, outer cuneiform.

u, 'unciforme' do. of *b*, cuboides; both of these representing two distinct carpals coalesced, as the scapholunar

* The tendon of the triceps femoris is not ossified in this species, where it passes over the knee-joint at 66′; it resembles in this respect its homotype, the tendon of the biceps brachii, in the fore-limb.

in the carpus represents the astragalus and scaphoid in the tarsus, and the calcaneum reciprocally the cuneiform and pisiform bones.

The serial homologies of the carpals and tarsals are better illustrated in the hand (fig. 13) and foot (fig. 14) of the orang, as has been before explained.

Having thus noticed some of the chief varieties of the mammalian modification of the vertebrate archetype, there remains to add only a few words in explanation of fig. 6,—the diagram of the human skeleton.

As this is that which the anatomist has been accustomed to hear described most frequently and exclusively by the special terms, and according to the special views and ends of anthropotomy, the language in which its deviations from the common archetype have now to be noticed will probably appear strange and bizarre. The comprehension of the explanation will be facilitated by reference to the special name of the bone through its numeral in the column of names whenever such bone is alluded to under its general or archetypal name.

In the first and, notwithstanding the upright posture, the most anterior of the cranial segments, by reason of their forward curvature, the hæmapophysis (21) coalesces early with its own moiety of the divided spine (22), and the same thing happens to the next hæmal arch (29) with subsequent obliteration of the symphysis between the halves of its spine (32).

The pleurapophysis (20) of the first arch remains a distinct bone: its diverging appendage (24) coalesces with and becomes a 'process' of the centrum (5) of the parietal vertebra.

The neurapophyses (14) of the anterior segment are modified as in other mammalia, *i. e.* become confluent together and with the olfactory capsules; but appear externally below the orbital process of the frontal.

The spine (15) is small, but bifid.

That of the second segment (11) attains its maximum of development, as do also the spines of the two following vertebræ (7 and 3). The bifid spine of the parietal segment is truly enormous as compared with that of the fish (fig. 2, 7) or the reptile (fig. 3, 7), in which latter animal the spine, being undivided, adheres closer to the archetype.

The diverging appendage (26, 27) from the hæmapophysis (21) is divided into two pieces, as in most mammals and reptiles; both are broad and flat: the first (26) serves to fix the arch to the parapophysis (12) of the second segment, from which it is here dislocated; the portion (27), which becomes enormously expanded, covers a large vacuity between the third and fourth neural arches, and overlaps by a squamous suture part of the expanded spines of both those vertebræ. It also anchyloses below with the pleurapophysis (28) of the second segment, with the parapophysis (8) and the pleurapophysis (38) of the third segment, as well as with the bony capsule of the organ of hearing (16), forming with those parts the most singularly complex 'cranial bone'—the 'os temporis' of anthropotomy.

The centrums (5, 9) and neurapophyses (6, 10) of the second and third segments coalesce with each other, and with the first pair of diverging appendages (24) of the anterior hæmal arch (20, 21, 22), forming the complex 'sphenoid' bone of anthropotomy.

The centrum (1), neurapophyses (2), and neural spine (3) of the fourth segment speedily anchylose together, and their centrum afterwards coalesces with that (5) of the parietal vertebra, forming the still more complex cranial bone called 'os spheno-occipitale' by Soemmering.

The hæmapophyses of the third much-reduced hæmal arch (40) are ossified only at the extremity which joins the spine (41): the remainder of the hæmapophysis is continued in a ligamentous state to their anchylosed pleurapophyses (38), forming the 'styloid processes of the temporal bone.'

The detached and displaced pleurapophyses (51) of the occipital vertebra attain considerable breadth: their hæmapophyses (52) are ossified only at the extremity which joins the pleurapophysis, and with which it coalesces. The diverging appendage (53–57) here attains its maximum of adaptive development; as in the skate-fish (*Raia*) it exhibits the extreme of vegetative or polaric growth. But the progressive steps by which it departs from the primitive or archetypal simplicity, shown in figures 7 and 8, are so gradual, that the special homology of the arm and hand of man with the bifid-jointed appendage of the scapular arch in the amphiuma, and with the simple jointed ray of that of the scapular arch of the lepidosiren, has never been doubted or called in question. In ascending, therefore, to the higher generalization of the significa-

tion, or relation to the archetype, of such simple, or bifid, jointed or more complicated appendage of such scapular arch, we are compelled by the truth, as it exists in nature, to admit that the scapular arch in the lepidosiren and other fishes forms the inferior costal or hæmal arch of the occipital segment or vertebra; and, by reference to the archetype, to see in the diverging appendage of such arch, a repetition of similarly simple diverging appendages of succeeding segments. These, indeed, retain their primitive simplicity, as shown in the trunk-vertebræ of the fish (fig. 2, *a a*) and of the bird (fig. 4, *a a*); and that simplicity is very gradually departed from in the case of the appendages of the occipital vertebra, by the stages recognisable in figs. 7 and 8. If, then, it be admitted that the upper limb (arm and hand) of man is the homologue of the fore-limb of the amphiume, of the pectoral fin of the fish and of the pectoral ray of the lepidosiren; it follows, that, like the latter, it must also be the 'diverging appendage' of the arch called 'scapular,' which is the hæmal arch of the occipital vertebra; and, therefore, however strange or paradoxical the proposition may sound, that the scapular arch and its appendages, down to the last phalanx of the little finger, are truly and essentially bones of the skull.

The centrum of the first segment of the neck is subject to the same modification as in the ordinary mammalia, the major part (*c a*) remaining anchylosed to the centrum of the succeeding segment (*c d*), of which it forms the 'odontoid process' in human anatomy. The inferior cortical part (*c, a, x*), or 'hypapophysis,' is that which is usually called the 'body' of the atlas: it is connected by aponeurosis to the corresponding part of the centrum of the occipital vertebra: the articulation of the head with the neck is chiefly by means of zygapophyses developed in the form of convex condyles from the neurapophyses (2), and received by the concave zygapophyses of the neural arch of the atlas. In the other cervical segments, the autogenous elements of which they are composed are represented diagrammatically in fig. 6 as distinct, viz. the centrum, neurapophysis, neural spine, and pleurapophysis; the latter element in the seventh vertebra sometimes attains a length nearly equal to that of the first dorsal. The hæmapophyses of the atlas (5s: see also fig. 2, 5s) are wholly ossified and well-developed.

In the seven vertebræ which succeed the cervicals the pleur-

apophyses (*pl*) are progressively elongated; they are shifted from their proper centrum to the interspace between it and the next segment above, or in advance, and retain their moveable joints. The hæmapophyses (*h*) are cartilaginous and articulate with the ends of the pleurapophyses and with the hæmal spines (*hs*), which are flattened, slightly expanded, and ultimately blended into one bone called 'sternum.' The hæmal spine of the first thoracic segment remains longest distinct: it receives, also, the extremities of the displaced hæmapophyses (53), and has been called 'manubrium sterni.' The hæmal spine of the seventh segment commonly continues longer distinct, and is later in becoming ossified, whence it is called 'ensiform cartilage': it probably includes the rudiments of some succeeding hæmal spines. In the four succeeding segments the pleurapophyses become progressively shorter, and the hæmapophyses, still cartilaginous, are severally attached by their lower attenuated ends to the pair in advance; leaving the hæmal arch incomplete below. In the next vertebra (19th from the skull) the still shorter pleurapophyses resume the exclusive articulation with their proper centrum; and the correspondingly short and pointed hæmapophyses are appended to their extremities and terminate freely.

Those pleurapophyses and hæmapophyses which directly articulate with hæmal spines (sternum) are called collectively 'true ribs' (costæ veræ), the proximal element being 'the bony part of the rib' (pars ossea costæ), the distal one 'the cartilage of the rib.' The rest of the hæmal arches which are incomplete through the absence of the hæmal spine, are called 'false ribs' (costæ spuriæ); and the last, which terminates freely in the origin of the diaphragm, is a 'floating rib.' The centrum, neurapophyses, and neural spine of each segment with freely articulated pleurapophyses coalesce into one bone, called 'dorsal vertebra' in anthropotomy: these vertebræ are twelve in number. Each of the five succeeding segments is represented by the same elements (centrum and neural arch) coalesced that constitute the so-called dorsal vertebræ: they are called 'lumbar vertebræ': they have no distinct ossified pleurapophyses, but rudiments of such are connate with and lengthen out the diapophyses. The hæmal arches in the abdominal region retain their aponeurotic texture: the anchylosed and stunted pleurapophyses are continued by the tendinous origins of the 'transversus abdominis'; the hæmapophyses are the 'in-

scriptiones tendineæ recti abdominis;' and the basis of the hæmal spines is the 'linea alba.' Certain elements of the five succeeding segments coalescing together in the progress of growth form the bone called 'sacrum,' and are described individually as sacral vertebræ. The first four of these each combine the same elements, coalesced, as in the neck; viz. centrum, neurapophyses, neural spine, and short but thick pleurapophyses*. One typical segment, the second, is completed by the meeting of the broad sides of the inverted arch (62, 63, 64) at the 'ischio-pubic symphysis' forming the 'pelvis' of anthropotomy.

The first sacral vertebra has its hæmapophysis (64, *pubis*) ossified, but separated from its proper pleurapophysis by the expanded (iliac) portion of that of the succeeding vertebra, with which it coalesces, as well as with the hæmapophysis (ischium) of the same vertebra.

The second sacral vertebra has its pleurapophysis divided, and the lower portion expanded to form the so-called 'ilium' (62). The hæmapophysis (63) coalesces with that of the preceding vertebra (64), and with its own pleurapophysis (62, fig. 6).

The short and thick pleurapophyses of the third sacral vertebra also articulate in the adult with the expanded distal portions of those of the second sacral vertebra: but these (iliac bones) are restricted in infancy and early childhood to their connections with the first and second sacral vertebræ, which connections are permanent in most reptiles (fig. 3).

The fourth sacral vertebra consists of centrum, neurapophyses, and rudimental pleurapophyses; the fifth sacral vertebra of centrum and rudimental neurapophyses, which rarely meet above the neural canal.

In each sacral vertebra the elements of the neural arch and rudimental ribs first coalesce together; and afterwards the vertebræ unite with each other and form the anthropotomical bone called 'sacrum.'

The first coccygeal vertebra in man consists of a centrum and of stunted exogenous neurapophyses† wide apart above, but deve-

* J. Müller notices the rudimental ribs in the first and second sacral vertebræ of the human fœtus in his 'Anatomie der Myxinoiden,' heft i. 1834, p. 240. Mr. Carlile has described (Report of British Association, 1837, p. 112), and Dr. Knox has figured (Lancet, 1839, p. 191), these ribs and their homotypes in the third and fourth sacral vertebræ.

† "Shoulders of the os coccygis."—Monro, *l. c.* p. 142.

loping zygapophyses, which join those of the last sacral vertebra, and diapophyses which extend outwards further than those of the same vertebra. The neurapophyses are represented by exogenous tubercles of bone in the second coccygeal vertebra; and the third and fourth vertebræ are reduced to the centrums only.

The cartilaginous deposits in the primitive blastema of this extremity of the trunk indicate a greater number of caudal vertebræ, and the rudimental tail is proportionally longer in the embryo than in the adult. It is shortened, however, by absorption prior to the commencement of ossification, and but four segments are indicated by depositions of the earthy salts in the situations proper to the above-specified elements of a typical vertebra: these finally coalesce into a single bone "of a crooked pyramidal figure," which got its name of 'os coccygis' from its supposed resemblance to a cuckoo's beak*.

The early recognition of these and other specialities arising out of the various adaptive modifications of the typical segments of the human skeleton found its expression, necessarily, in special terms, the convenience of which will ensure their permanence; but the progress of anatomical science having unfolded the primary form which is the basis of those modifications, there arises the same necessity for giving utterance to ideas of the generic character of the parts by general terms.

Inasmuch, however, as the different segments of the human skeleton deviate in various degrees from the common archetype, and as the different elements of such segments differ in their modifiability, anthropotomy has at no period wanted also its 'general terms' expressive of the recognised extent of such conformity: such terms also, indicating, obscurely indeed, so much perception of the pre-existing model as could be obtained from the study of one form, at a period when that form—the human frame—was viewed as something not only above, but distinct from, if not antithetical to the structures of the brute creation, and when it was little suspected that all the parts and organs of man had been sketched out, in anticipation, so to speak, in the inferior animals. Thus the word 'vertebra' shows, by the number of the segments or parts of segments to which it is applied in anthropotomy, a recognition of the degree in which the principle of repetition of similar parts more obviously prevails in the construc-

* Monro, *l. c.* p. 141.

tion of the human endoskeleton. And, inasmuch as in some regions (the cervical, *e. g.*) the 'vertebra' includes all the elements of the typical segment, there developed, it has been retained in homological anatomy, but, with a more consistent and definite meaning, as the technical term of the primary segment of the endoskeleton in all vertebrate animals.

The 'true vertebræ' of anthropotomy are those segments which retain the power of moving upon each other; and the term is applied in a peculiar and empirical sense very different from the meaning which the anatomist attaches to a true or typical vertebra. The 'false vertebræ' of anthropotomy are those segments or parts of segments forming the lower or hinder extreme of the endoskeleton, and which do not admit of reciprocal motion at their joints. And Monro, admitting that the condition of even the human os coccygis sometimes militates against the definition, meets the objection by arguing for the speciality of that bone, and with as good or better reason than those who have subsequently contended against admitting the cranial segments into the category of vertebræ. "From the description of this bone" (os coccygis), "we see how little it resembles *vertebræ*; since it seldom has processes, never has any cavity for the spinal marrow, nor holes for the passage of nerves*."

Embryology has since demonstrated that the parts of the os coccygis are originally in vertebral relation with the neural axis; and that this is subsequently shortened by a concentrative movement, which in like manner withdraws it from the terminal segment at the opposite extreme of the endoskeleton. The homology of the divisions of the sacrum with the true vertebræ is admitted by Monro, because of the perforations for the nerves: and this character is still retained in the nasal vertebra in the form of the cribriform foramina, although its neurapophyses, like those of the sacrum, have lost their primitive relation to the neural axis.

Homological anatomy, therefore, teaches, that the term 'vertebra' should not only be applied to the segments of the human skeleton in the technical and definite sense illustrated by figs. 7 and 8, pp. 42 & 43, but be extended to those modified and reciprocally immoveable segments which terminate the endoskeleton superiorly, in Man, and are called collectively 'skull.' (figs. 1 to 6, Cr.)

The term 'head,' then, indicates a region of specially modified

* Monro, *l. c.* p. 143.

vertebræ, like the terms 'neck,' 'chest,' 'loins,' &c.; and amongst the groups of the primary segments characterized by specific modifications, the 'cranial' vertebræ must be added to the 'cervical,' 'thoracic or dorsal,' 'lumbar,' 'sacral,' and 'coccygeal or caudal.'

Such, with reference to the 'general' term 'vertebra,' seems to be the advance of which anthropotomical science is susceptible, in order to keep pace and be in harmony with anatomy.

As to the elements of the typical vertebra, anthropotomy has also its general phrases (see Table II. column vi. 'Soemmering,' in my Work 'On the Archetype of the Vertebrate Skeleton'), some of which are equivalent to the clearly-defined technical terms of such elements in anatomy properly so called.

The serial homology of the centrum (*corpus vertebræ*) has been recognised in all the so-called 'true vertebræ,' and in some of the 'false vertebræ': thus Monro says, "The fore-part of the *os sacrum*, analogous to the bodies of the true vertebræ, is smooth and flat*." But their smooth and flat homotypes in the skull have only the special names of 'basilar' and 'cuneiform' processes; of 'processus azygos' and 'vomer.' The 'neurapophyses' are recognised as repetitions of the same part under the definitions of 'a bony bridge produced backwards from each side of the body of the vertebra,' of '*arcus posterior vertebræ*,' of 'vertebral laminæ' or 'pedicles.' Monro describes these rudimental elements in the last sacral vertebra, where they are 'exogenous,' as 'knobs,' and in the first coccygeal vertebra as its 'shoulders.' In the skull they receive the special definitions of "the pieces of the occipital bone situated on each side of the great foramen; from which nearly the whole condyles are produced†" (*partes laterales seu condyloideæ*, Soem.); 'great' or 'temporal wings of the sphenoidal bone'‡; 'orbitar wings' or 'processes of the sphenoidal bone;' 'nasal' or 'vertical plate' and 'crista galli' of the ethmoid ('*pars media ossis æthmoidei*,' Soem.).

The neural spines are called generally '*spinal processes*' in every segment of the trunk: in the head they are known only by the special names of 'occipital plate,' 'parietal bones,' 'frontal bone,' 'nasal bones.'

The pleurapophyses, when free, long, and slender, are called 'ribs,' 'vertebral ribs,' or 'bony parts of the ribs'; when short

* Monro, *l. c.* p. 138. † *L. c.* p. 76. ‡ *L. c.* p. 86.

and anchylosed, they are called, in the neck, "the second transverse processes that come out from the sides of the body of each vertebra*;" (*radix prior processus transversi vertebræ*, Soem. ;) in the sacrum, 'transverse processes' and 'ilium'; in the skull, 'scapula,' 'styloid process of the temporal bone,' 'external auditory or tympanic process of the same bone;' 'palatine bone.'

In like manner the serial homology of the hæmapophyses is recognised in the thoracic region by the general term 'cartilages of the ribs' or 'cartilages of the sternum'† there applied to the same elements of twelve successive segments. When ossified in other vertebræ they have received the special names of 'ischium,' 'pubis,' 'coracoid process of the scapula,' 'clavicle,' 'appendix or lesser cornua of the hyoid bone,' ('*crura superiora*,' '*os linguale superius*,' Soem.), 'lower jaw' or *mandibula*, 'upper jaw' or *maxilla*.

The exigences of descriptive anthropotomy and its highly important applications to Medicine and Surgery necessitate such special nomenclature, and the reform which that nomenclature chiefly requires is the substitution of names in the place of phrases for the parts of the human body.

But the retention and use of specific names for specially modified elements in the different segments by no means preclude the entertainment of general ideas and the necessity of expressing them by generic names for the homologous elements in the entire series of vertebræ.

If anthropotomy is to make corresponding progress with anatomy, and to derive the same light from the generalizations of zootomical science which medical botany has derived from general botanical science, its nomenclature must expand to receive those generic terms which express the essential nature of the parts, heretofore named and known only according to the results of parti-

* Monro, *l. c.* p. 126.

† Laurentius, in describing the human thoracic pleurapophyses, says, "Earum duplex est articulatio, altera cum spondylis dorsi, altera cum sterni cartilaginibus" (Anatomica Humani Corporis, Fol. 1600, p. 94). The perception of the essential distinctness of the vertebral ribs had not then been blunted by the constant repetition of the conventional idea of their forming an ossified part of a whole, *i. e.* a rib, completed by the hæmapophysis under the name of the 'cartilago costæ.' In birds it is not uncommon to find the hæmapophyses not only ossified, but some of them attached to the sternum, and detached from the pleurapophyses.

cular and insulated observation. A term which truly expresses the general homology of a part enunciates the most important and constant characters of such part throughout the whole animal series, and implies therefore a knowledge of such characters in that part of the human body, when used and understood by the human anatomist. Before the cuneiform process of the occipital bone could be defined as the 'occipital centrum,' the modifications and relations of the homologous part in all classes of vertebrate animals had to be accurately determined. The generic homological term expresses the sum or result of such comparisons, and the use of such terms by the anthropotomist implies his knowledge of the 'idea' or primal pattern of the human frame supporting the modifications that raise it to an eminence so far above those of all other vertebrate animals.

In no species, however, is each segment of the endoskeleton so plainly impressed with its own individual characters, as in Man; the practised anthropotomist, for example, will at once select and name any given vertebra from either the cervical, the dorsal, or the lumbar series. During that brilliant period of human anatomy which was illuminated by a Fabricius, an Eustachius, a Fallopius, and a Laurentius, the terms expressive of the recognition of such specific characters were more numerous and often more precise than in our modern compilations. Pleurapophyses were individualized in the thorax as well as in the head: the 'antistrophoi,' 'stereai' and 'sternitides,' for example, were distinguished from the other 'pleurai gnesiai'*.

General anatomical science reveals the unity which pervades the diversity, and demonstrates the whole skeleton of man to be the harmonized sum of a series of essentially similar segments, although each segment differs from the other, and all vary from their archetype.

* Anatomica Humani Corporis, &c., multis controversiis et observationibus novis illustrata. Andr. Laurentio, fol. 1600, p. 95.

THE END.

Printed by Richard and John E. Taylor, Red Lion Court, Fleet Street.

Alt.ª Nomina.

1. Basioccipitale
2. Exoccipitale
3. Supraoccipitale
4. Paroccipitale
5. Basisphenoideum
6. Alisphenoideum
7. Parietale
8. Mastoideum
9. Presphenoideum
9'. Entosphenoideum
10. Orbitosphenoideum
11. Frontale
12. Postfrontale
13. Vomer
14. Prefrontale
15. Nasale
16. Petrosum
17. Scleroticum
18. Ethmoturbinale
19. Turbinale
20. Palatinum
21. Maxillare
22. Premaxillare
23. Entopterygoideum
24. Pterygoideum
25. Ectopterygoideum
26. Malare
27. Squamosum
28. Tympanicum
28a. Epitympanicum
28b. Mesotympanicum
28c. Pretympanicum
28d. Hypotympanicum
29. Articulare
29'. Surangulare
30. Angulare
31. Splenium
31'. Coronoideum
32. Dentarium
29.32. Mandibula
34. Preoperculum
35. Operculum
36. Subopperculum
37. Interoperculum
38. Stylohyale
39. Epihyale
40. Ceratohyale
41. Basi-hyale
42. Glosso-hyale
43. Urohyale — 44. Branchiostegum
50. Suprascapula — 46. Thyrohyale
51. Scapula
52. Coracoideum — 52'. Episternum
53. Humerus
54. Ulna
55. Radius
56. Carpus
57. Metacarpus, phalanx
58. Clavicula — 59. Manubrium
62. Ilium — 60. Sternum
63. Ischium — 61. Xiphisternum
64. Pubis
65. Femur
66. Tibia
66'. Patella
67. Fibula
67'. Fabella
68. Tarsus
69. Metatarsus, phalanx.

ns. Spina

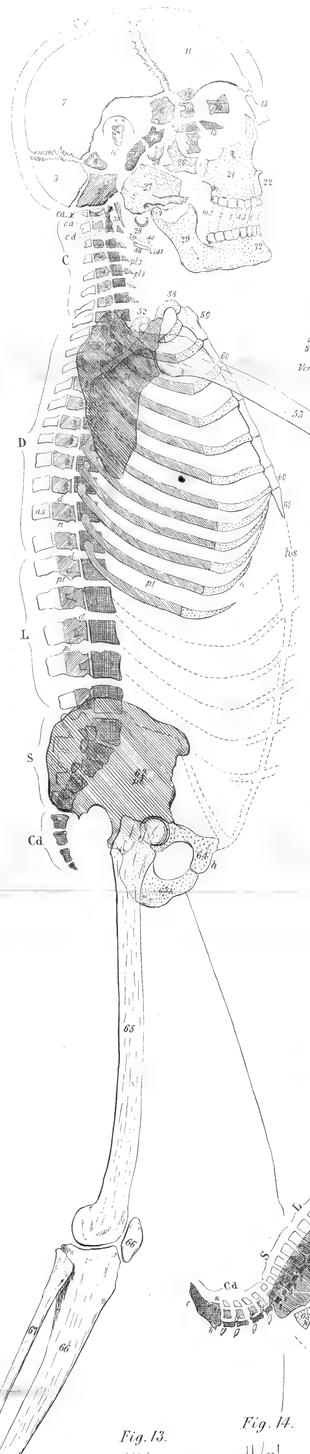


Fig. 6. Homo.

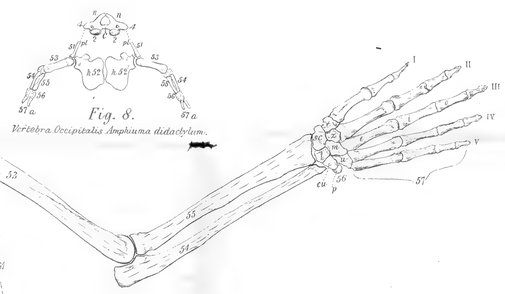


Fig. 8.
Vertebra Occipitalis Amphiuma didactylum.

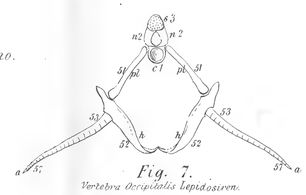


Fig. 7.
Vertebra Occipitalis Lepidosiren.

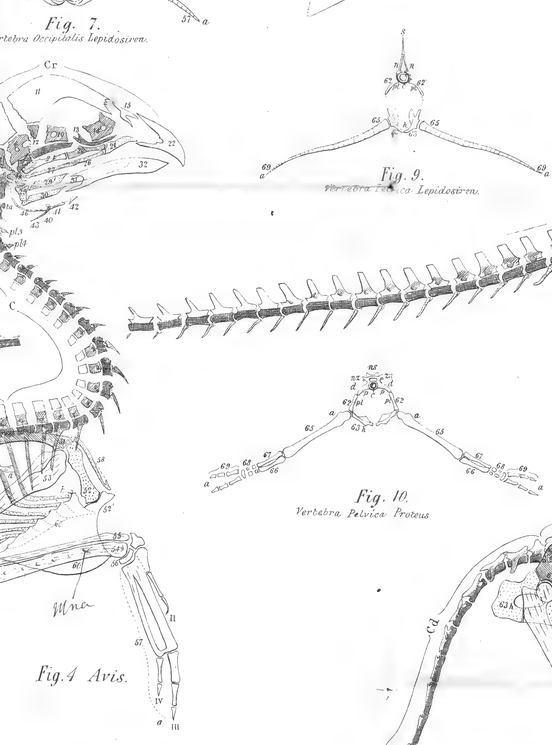


Fig. 1. Archetypus.

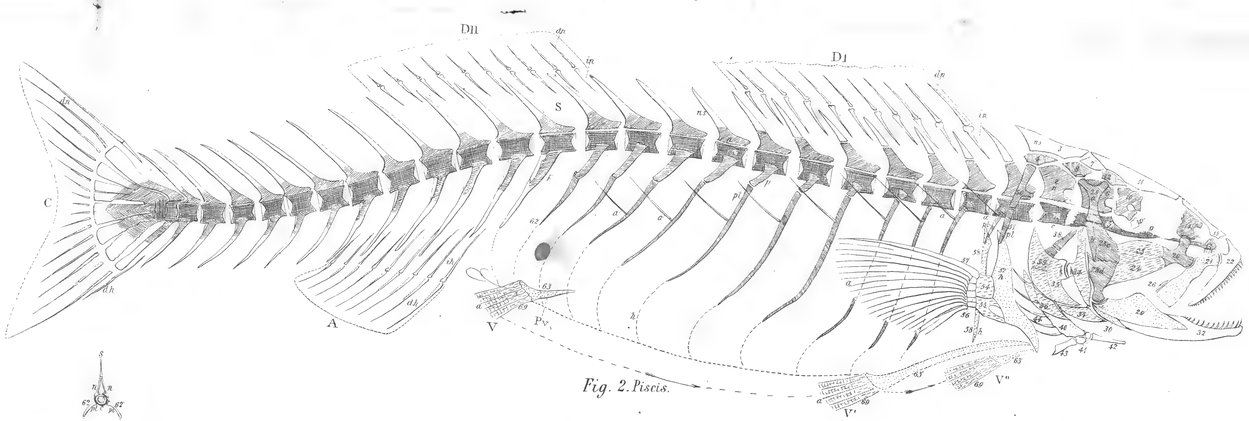


Fig. 2. Piscis.

Fig. 9.
Vertebra Pelvica Lepidosiren.

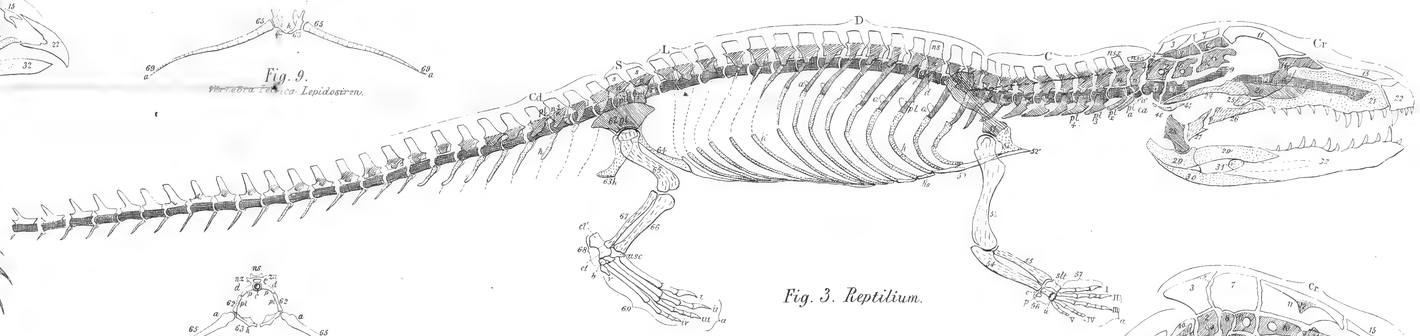


Fig. 3. Reptilium.

Fig. 10.
Vertebra Pelvica Proteus

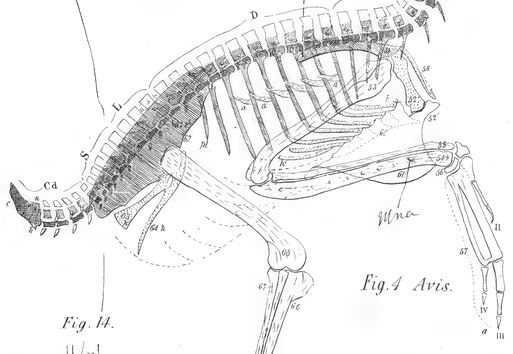


Fig. 4 Avis.

Fig. 13.

Fig. 14.

Fig. 5. Mammale

Fig. 17.
Rhinoceros.

Fig. 18.
Bos.

Fig. 19.
Equus.

28a. *Epitympanicum*
28b. *Mesotympanicum*
28c. *Pretympanicum*
28d. *Hypotympanicum*
29. *Articulare*
29'. *Surangulare*
30. *Angulare*
31. *Spleniun*
31'. *Coronoideum*
32. *Dentarium*
29.32. *Mandibula*
34. *Preopereulum*
35. *Operculum*
36. *Subopereulum*
37. *Interopereulum*
38. *Stylohyale*
39. *Epihyale*
40. *Ceratohyale*
41. *Basi hyale*
42. *Glosso-hyale*
43. *Urohyale* 44. *Branchiostegum*
50. *Suprascapula* 46. *Thyrrhyale*
51. *Scapula*
52. *Coracoideum* 52'. *Episternum*
53. *Humerus*
54. *Ulna*
55. *Radius*
56. *Carpus*
57. *Metacarpus, phalanx*
58. *Clavicula* 59. *Manubrium*
62. *Ilium* 60. *Sternum*
63. *Ischium* 61. *Xyphisternum*
64. *Pubis*
65. *Femur*
66. *Tibia*
66'. *Patella*
67. *Fibula*
67'. *Fabella*
68. *Tarsus*
69. *Metatarsus, phalanx.*

ns *Spina*
n *Neurapophysis*
d *Diapophysis*
c *Centrum*
p *Parapophysis*
pl *Pleurapophysis*
h *Hæmapophysis*
hs *Spina*
a *Appendix*

R.O. DEL.

Fig. 7.
Vertebra Occipitalis Lepidosiren.

Fig. 2. Pisces.

Fig. 9.
Vertebra Pelvica Lepidosiren.

Fig. 3. Reptilium.

Fig. 10.
Vertebra Pelvica Proteus

Fig. 4 Avis.

Fig. 5. Mammale

Fig. 11.
Struthio.

Fig. 12. Emys.

Fig. 13.
Pithecus

Fig. 14.

Fig. 15.

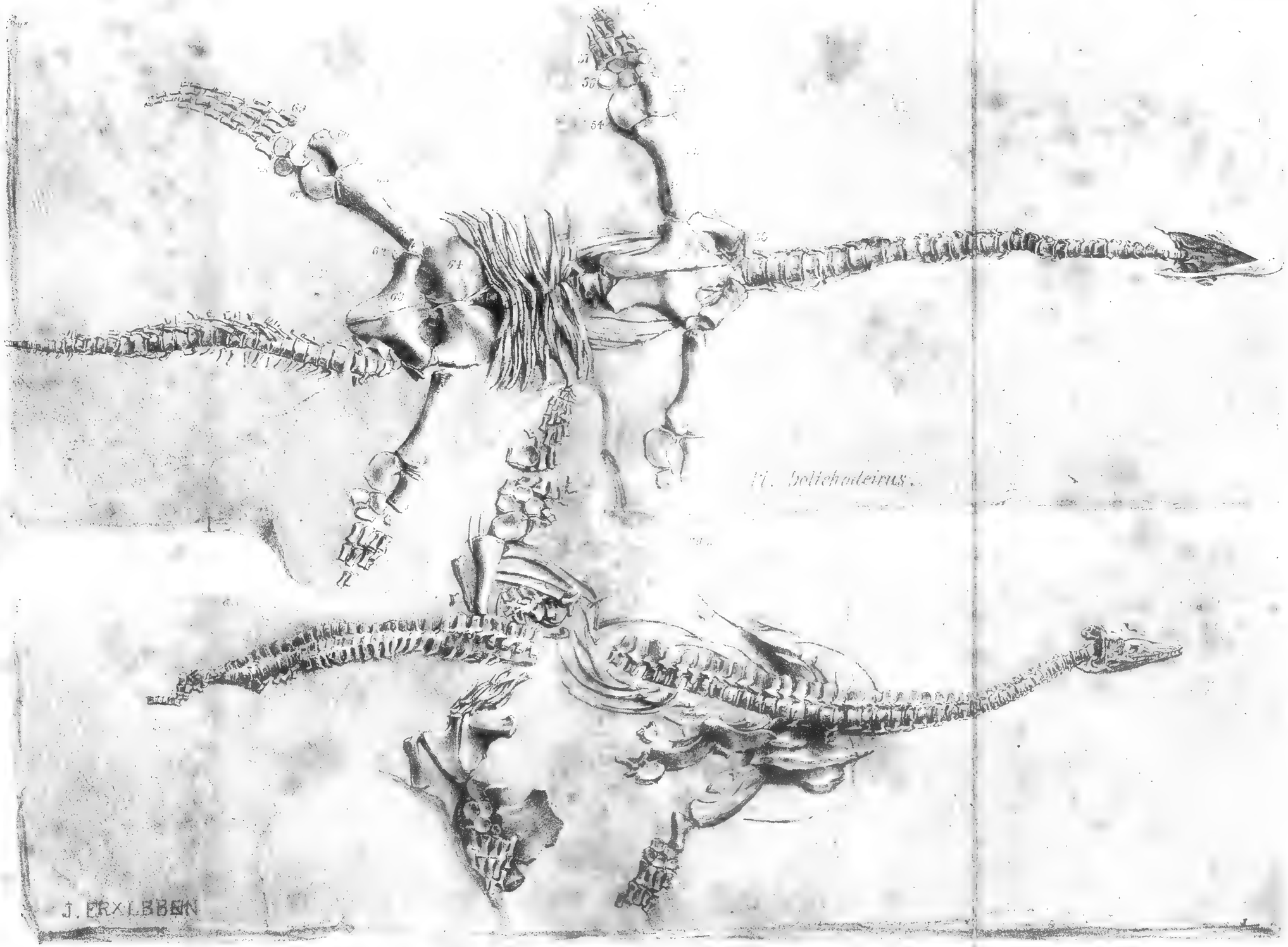
Fig. 16
Phascolomys.

Fig. 17.
Rhinoceros.

Fig. 18.
Bos.

Fig. 19.
Equus.

TUFFEN WEST, LITH.



Plesiosaurus Hawkinsii.

London, June, 1848.

BOOKS PUBLISHED BY MR. VAN VOORST.

The Illustrations to the Works enumerated in this Catalogue have been designed or drawn and engraved expressly for the Works they respectively embellish, and they are never used for other Works.

Illustrated Reprints.

WATTS' DIVINE AND MORAL SONGS. With 30 Illustrations by C. W. COPE, A.R.A.; engraved by JOHN THOMPSON. Square 8vo., 7*s.* 6*d.* or 21*s.* in morocco.

Uniform with the above,

THE VICAR OF WAKEFIELD. With 32 Illustrations by WILLIAM MULREADY, R.A.: engraved by JOHN THOMPSON. 1*l.* 1*s.* square 8vo, or 36*s.* in morocco.

Also of Uniform size,

SHAKSPEARE'S SEVEN AGES OF MAN. Illustrated by WILLIAM MULREADY, R.A.; J. CONSTABLE, R.A.; SIR DAVID WILKIE, R.A.; W. COLLINS, R.A.; A. E. CHALON, R.A.; A. COOPER, R.A.; SIR A. W. CALLCOTT, R.A.; EDWIN LANDSEER, R.A.; W. HILTON, R.A. 6*s.*

A few copies of the First Edition in 4to. remain for sale.

THE FARMER'S BOY AND OTHER RURAL TALES AND POEMS. By ROBERT BLOOMFIELD. With Thirteen Illustrations by SIDNEY COOPER. R.A., HORSLEY, FREDERICK TAYLER, and THOMAS WEBSTER, R.A. A few copies on large paper, of a size to correspond with the above, price 15*s.* (Small Paper copies, 7*s.* 6*d.*)

GRAY'S ELEGY IN A COUNTRY CHURCH-YARD. Each stanza Illustrated with an Engraving, from 33 original drawings by the most eminent Artists. Post 8vo., price 9*s.* cloth. A Polyglot Edition of this Volume, with inter-paged Translations in the Greek, Latin, German, Italian, and French Languages. Price 12*s.* And of uniform size.

THE BARD. By GRAY. With Illustrations by the HON. MRS. JOHN TALBOT. Post 8vo. 7*s.*

A CABINET EDITION OF THE HOLY BIBLE; The Authorized Version. With 24 highly-finished Steel Engravings. In embossed binding, 10*s.* 6*d.* And uniform,

THE BOOK OF COMMON PRAYER. With 10 Engravings. In embossed binding, 4*s.*

A CABINET EDITION OF THE ECONOMY OF HUMAN LIFE. In Twelve Books. By R. DODSLEY. With 12 Plates engraved on steel, from original designs, 18mo. 5*s.*

AIKIN'S CALENDAR OF NATURE; or, Natural History of each Month of the Year. With additions, by a Fellow of the Linnæan and Zoological Societies, and 18 designs by Cattermole. Small 8vo., 2*s.* 6*d.*

Architecture.

ARCHITECTURAL PARALLELS; or, The Progress of Ecclesiastical Architecture in England, through the Twelfth and Thirteenth Centuries, exhibited in a Series of Parallel Examples selected from Abbey Churches. By EDMUND SHARPE, M.A. 121 Plates in tinted outline, each 18 in. by 12 in., half mor. 13*l.* 13*s.*, or large paper, 16*l.* 10*s.*

INSTRUMENTA ECCLESIASTICA: a Series of Seventy-two designs for the Furniture, Fittings, and Decorations of Churches and their Precincts. Edited by the Ecclesiological, late Cambridge Camden Society. 4to. 1*l.* 11*s.* 6*d.*

A MANUAL OF GOTHIC MOLDINGS. A Practical Treatise on their Formation, Gradual Development, Combinations, and Varieties; with full Directions for copying them, and for determining their Dates. By F. A. PALEY, M.A. Second Edition, Illustrated by nearly 600 Examples. 8vo. 7*s.* 6*d.*

Other Works by MR. PALEY.

THE CHURCH RESTORERS; A Tale, Treating of Ancient and Modern Architecture and Church Decorations. With a Frontispiece. Foolscap 8vo. 4*s.* 6*d.*

A MANUAL OF GOTHIC ARCHITECTURE. With a full Account of Monumental Brasses and Ecclesiastical Costume. Foolscap 8vo., with 70 Illustrations, 6*s.* 6*d.*

BAPTISMAL FONTS. A Series of 125 Engravings, Examples of the different Periods, accompanied with Descriptions; and with an Introductory Essay. In 8vo. 1*l.* 1*s.*

DECORATED WINDOWS. By EDMUND SHARPE, M.A., Architect. Each Part, price 2*s.* 6*d.*, will contain Eight Examples selected from the Parish Churches of England, engraved on Steel, with accompanying Descriptions; the concluding part will be Introductory, and Illustrated by Woodcuts, &c.

PERRAN-ZABULOE; with an Account of the Past and Present State of the Oratory of St. Piran-in-the-Sands, and Remarks on its Antiquity. By the REV. WM. HASLAM, B.A., Resident Curate. Foolscap 8vo., with several Illustrations, 4*s.* 6*d.*

HERALDRY OF FISH. By THOMAS MOULE. The Engravings, 205 in number, are from Stained Glass, Tombs, Sculpture, and Carving, Medals and Coins, Rolls of Arms, and Pedigrees. 8vo., price 21*s.* A few on large paper (royal 8vo.) for colouring, price 2*l.* 2*s.*

Natural History.

THE ISLE OF MAN; its History, Physical, Ecclesiastical, Civil, and Legendary. By the REV. J. G. CUMMING, M.A., F.G.S., Vice-Principal of King William's College, Castletown. Post 8vo., with Illustrations, 12*s.* 6*d.*

PROFESSOR OWEN ON THE ARCHETYPE AND HOMOLOGIES OF THE VERTEBRATE SKELETON. 8vo. 10*s.*

A SYSTEMATIC CATALOGUE OF THE EGGS OF BRITISH BIRDS, arranged with a View to supersede the use of Labels for Eggs. By the Rev. S. C. MALAN, M.A., M.A.S. On writing-paper. 8vo. 8*s.* 6*d.*

RARE AND REMARKABLE ANIMALS OF SCOTLAND, Represented from Living Subjects: with Practical Observations on their Nature. By SIR JOHN GRAHAM DALYELL, BART. Vol. First, 53 Coloured Plates, 4to., 3*l.* 3*s.*

JOHN VAN VOORST, 1, PATERNOSTER ROW.

the Botany School

GEOLOGY: Introductory, Descriptive, and Practical. By DAVID THOMAS ANSTED, M.A., F.R.S.; Fellow of Jesus College, Cambridge; Professor of Geology in King's College, London. 2 Vols. 8vo., with numerous Illustrative Engravings, price 2*l.* 2*s.*

THE BIRDS OF JAMAICA. By P. H. GOSSE, Author of the "Canadian Naturalist," &c. Post 8vo., price 10*s.*

ILLUSTRATIONS to this Work of the Species not heretofore figured, Imperial 8vo., to be completed in about 15 Parts, at 2*s.* 6*d.* Each Part will contain Four Birds Coloured.

OBSERVATIONS IN NATURAL HISTORY; with a Calendar of Periodic Phenomena. By the REV. LEONARD JENYNS, M.A., F.L.S. Post 8vo, 10*s.* 6*d.*

ILLUSTRATIONS OF INSTINCT, deduced from the Habits of British Animals. By JONATHAN COUCH, F.L.S., Member of the Royal Geological Society and of the Royal Institution of Cornwall, &c. Post 8vo. 8*s.* 6*d.*

THE ANCIENT WORLD; or, Picturesque Sketches of Creation. By D. T. ANSTED, M.A., F.R.S., F.G.S., Professor of Geology in King's College, London, &c. &c. A New Edition, Post 8vo., with 149 Illustrations, 10*s.* 6*d.*

OUTLINES OF STRUCTURAL AND PHYSIOLOGICAL BOTANY. By ARTHUR HENFREY, F.L.S., Lecturer on Botany at the Middlesex Hospital; late Botanist to the Geological Survey of the United Kingdom. With 18 Plates, Foolscap 8vo. 10*s.* 6*d.*

A MANUAL OF BRITISH BOTANY; containing the Flowering Plants and Ferns, arranged according to the Natural Orders. By CHARLES C. BABINGTON, M.A., F.L.S., F.Z.S., &c. Second Edition, 12mo. 10*s.*

THE NATURAL HISTORY OF ANIMALS; By T. RYMER JONES, F.R.S., F.Z.S. Professor of Comparative Anatomy in King's College, London. Post 8vo., Vol. I., with 105 Illustrations, price 12*s.*

FIRST STEPS TO ANATOMY. By JAMES L. DRUMMOND, M.D., Professor of Anatomy and Physiology in the Belfast Royal Institution. With 12 Illustrative Plates. 12mo. 5*s.*

TRAVELS IN LYCIA, MILYAS, AND THE CIBYRATIS, in company with the late REV. E. T. DANIELL. By LIEUT. SPRATT, R.N. and PROFESSOR EDWARD FORBES. With numerous Illustrations, including Views of the Scenery; Plans of Ancient Cities and Buildings; Plates of Coins and Inscriptions; Cuts of Rock Tombs, Fossils, and Geological Sections, and an original Map of Lycia. 2 Vols. 8vo., 36*s.*

THE NATURAL HISTORY OF STAFFORDSHIRE, comprising its Geology, Zoology, Botany, and Meteorology; also its Antiquities, Topography, Manufactures, &c. By ROBERT GARNER, F.L.S. Illustrated, 8vo. 1*l.* 1*s.*

THE HONEY BEE; its Natural History, Physiology, and Management. By EDWARD BEVAN, M.D. A new Edition, 12mo., with Illustrations, 10*s.* 6*d.*

ON THE GROWTH OF PLANTS IN CLOSELY-GLAZED CASES. By N. B. WARD, F.L.S. 8vo., 5*s.*

A FAMILIAR INTRODUCTION TO THE HISTORY OF INSECTS. By EDWARD NEWMAN, F.L.S., F.Z.S., &c. 8vo. with nearly 100 Illustrations, price 12*s.*

WHITE'S NATURAL HISTORY OF SELBORNE. A new edition, with Notes, by the Rev. L. JENYNS, M.A., F.L.S. Fcp. 8vo., illustrated, 7*s.* 6*d.*

JOHN VAN VOORST, 1, PATERNOSTER ROW.

A FAMILIAR INTRODUCTION TO THE STUDY OF POLARIZED LIGHT; with a Description of, and Instructions for Using, the Table and Hydro-Oxygen Polariscope and Microscope. By CHARLES WOODWARD, F.R.S. 8vo., Illustrated, 3*s.*

ANATOMICAL MANIPULATION; or, The Methods of pursuing Practical Investigations in Comparative Anatomy and Physiology. Also an Introduction to the Use of the Microscope, &c. By ALFRED TULK, M.R.C.S., M.E.S.; and ARTHUR HENFREY, F.L.S., M.Mic.S. With Illustrated Diagrams. Foolscap 8vo., 9*s.*

THE NATURAL HISTORY OF GREAT BRITAIN. This Series of Works is Illustrated by many Hundred Engravings; every Species has been Drawn and Engraved under the immediate inspection of the Authors; the best Artists have been employed, and no care or expense has been spared. A few copies on larger paper, royal 8vo.

THE QUADRUPEDS, by PROFESSOR BELL. 1*l.* 8*s.*

THE BIRDS, By MR. YARRELL. Second Ed., 3 vols. 4*l.* 14*s.* 6*d.*

COLOURED ILLUSTRATIONS OF THE EGGS OF BIRDS, By MR. HEWITSON. 2 vols. 4*l.* 10*s.*

THE REPTILES, By PROFESSOR BELL. Second Edition, shortly.

THE FISHES, BY MR. YARRELL. Second Edition, 2 vols. 3*l.**

THE CRUSTACEA, By PROFESSOR BELL. Now in Course of Publication, in Parts at 2*s.* 6*d.*

THE STARFISHES, By PROFESSOR EDWARD FORBES. 15*s.*

THE ZOOPHYTES, By DR. JOHNSTON. Second Ed., 2 vols., 2*l.* 2*s.*

THE MOLLUSCOUS ANIMALS AND THEIR SHELLS, By PROFESSOR ED. FORBES, and MR. HANLEY. Now in Course of Publication, in Parts at 2*s.* 6*d.*; or Large Paper, with the Plates Coloured, 5*s.*

THE FOREST-TREES, By MR. SELBY. 28*s.*

THE FERNS AND ALLIED PLANTS, By MR. NEWMAN. 25*s.*

THE FOSSIL MAMMALS AND BIRDS, By PROFESSOR OWEN. 1*l.* 11*s.* 6*d.*

A GENERAL OUTLINE OF THE ANIMAL KINGDOM, By PROFESSOR T. RYMER JONES. 8vo. 1*l.* 18*s.*

---

* "This book ought to be largely circulated, not only on account of its scientific merits, but because it is popularly written throughout, and therefore likely to excite general attention to a subject which ought to be held as one of primary importance. Everyone is interested about fishes—the political economist, the epicure, the merchant, the man of science, the angler, the poor, the rich. We hail the appearance of this book as the dawn of a new era in the Natural History of England."—*Quarterly Review*, No. 116.

JOHN VAN VOORST, 1, PATERNOSTER ROW.

the Botany School